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# THE BOTANICAL GAZETTE

September 1911

Editor: JOHN M. COULTER

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THE
BOTANICAL GAZETTE

*SEPTEMBER 1911*

# A PRELIMINARY REPORT ON THE YEARLY ORIGIN AND DISSEMINATION OF PUCCINIA GRAMINIS

FREDERICK J. PRITCHARD

(WITH PLATE IV)

## Introduction

The annual reappearance of *Puccinia graminis* Pers., the black rust of cereals, and its dissemination among the various species of the Gramineae, have long remained obstinate problems. For nearly a century botanists and also agronomists, because of its economic importance, have endeavored to discover how this fungus passes the winter and spreads to the grain fields. A review of the literature, to bring out certain points which have been too much overlooked by those who are committed to the conception that the barberry is the sole source of spring infection, will be of interest in connection with the data which my own observations afford.

The barberry was considered a disseminator of rust by careful observers centuries ago. Even as early as 1660, as a result of their reports, an act of Parliament was passed at Rouen (**22**) condemning the use of this shrub in the vicinity of grain fields. A similar law was passed in Mass. (**28**) in 1755. Successive measures of this nature were subsequently enacted throughout Europe (**3**).

Proof of the influence of the barberry on rust contagion was furnished by SCHÖLER (**29**),[1] who in 1818 succeeded in infecting

[1] Cited by ERIKSSON.

rye with aecidiospores from barberry leaves. SCHÖLER's publication, however, remained buried until brought to light by NIELSON.

Infection of the barberry with *P. graminis* was not accomplished until 1865, when DE BARY (**3**) readily infected the young leaves with germinating sporidia, thus establishing the heteroecism of the organism. Unfortunately he was unable at the same time to germinate the mature aecidiospores, either fresh or after various periods of preservation, and hence the cereal host species was not reinfected, although the following year he accomplished this upon young rye plants.

The distance rust is spread from the barberry is variously estimated by different writers. MARSHALL (**24**),[2] who set large barberry bushes in the grain fields and made careful observations, states that the rust extended 10 yards in the direction of the prevailing wind. SCHÖLER (**29**), on the other hand, used small bushes and found that it scattered over an area of 30 to 40 square feet. Much greater distances are frequently recorded in the literature, although usually based upon casual observation or opinion. WITHERING (**33**),[3] for instance, advises that no barberry bushes should be planted within 300–400 yards of a grain field.

The absence of the barberry and *Mahonia* in several regions where *Puccinia graminis* is prevalent, as cited for Ecuador by LAGERHEIM (**21**), seems to indicate that the heteroecism of the fungus is merely facultative. According to BARCLAY (**1**), *P. graminis* is also commonly present in Jeypore, India, while the nearest barberry bushes are nearly 300 English miles distant. Moreover, "the aecidia are formed in summer, while the wheat and barley are grown in winter and harvested in April or May." In this same category ZUKAL (**34**) places Bosnia and Herzegovina, where, according to BRANDIS (**34**), the aecidial hosts, if present at all, are very rare. Perhaps the most striking case of this kind is in Australia, where *P. graminis* causes enormous damage to wheat, yet the barberry is not present and the aecidial stage has never been found.

The existence of a perennial mycelium, although established for a

[2] Cited by ARTHUR, Bull. Torr. Bot. Club **31**:113. 1904.

[3] Cited by ERIKSSON and HENNING (**16**).

number of rusts, has never been proved for *P. graminis*. ERIKSSON (**13, 14, 16**) found the mycelium scarcely extending beyond the contour of the pustules. DE BARY held that the development of the rust begins anew each year by the "germination of the teleutospores alone."

*P. graminis* was formerly considered one species capable of infecting various members of the Gramineae, and this supposedly wide range of infecting power was thought to conduce to its spread. ERIKSSON (**16**), however, after extensive inoculation experiments in Sweden, divides it into the following biological forms, which he finally classes as species:

Puccinia graminis secalis (Secale cereale, Hordeum vulgare, and Triticum repens).
Puccinia graminis avenae (Avena sativa).
Puccinia graminis tritici (Triticum vulgare).
Puccinia graminis airae (Aira caespitosa).
Puccinia graminis poae (Poa compressa).
Puccinia phlei-pratensis (Phleum pratense).

CARLETON'S (**10**) experiments in America, however, do not support ERIKSSON and HENNING'S results. He finds no distinction between the forms on wheat and barley. His results appear to establish two things: (1) "that the forms of black stem rust on wheat and barley, *Hordeum jubatum*, *Agropyron tenerum*, *A. Richardsoni*, and *Elymus canadensis glaucifolius*, are identical, with the probability that those on *Elymus virginicus muticus* and *Holcus lanatus* should be included; (2) that the black stem rust of *Agropyron occidentale* is physiologically distinct from any other."

Direct inoculation of the gramineous host with the germinating teleutospores has received some attention, although not as much as it deserves. Foremost among these experiments are probably those of DE BARY, who showed that the germinating sporidia of *P. graminis* would not infect the leaves of *Triticum vulgare*, *T. repens*, and *Avena fatua*. THÜMEN (**31**), however, asserts that the sporidia of *Melamspora salicina* infect the willow quite as easily as do the uredospores. PLOWRIGHT (**27**) also, in a detailed report, claims to have infected wheat plants directly with sporidia (teleutobearing straw), although he afterward informed KLEBAHN that

"his work rested upon an error." Other failures to infect wheat with germinating sporidia are reported by WARD (**32**) and ERIKSSON (**15**), though no mention is made of the number of trials nor the point of inoculation. Notwithstanding these failures, BREFELD (**8**) thinks further attempts should be made to infect young cereals with germinating teleutospores. His discovery that only the youngest tissues of cereals are penetrated by smut sporelings gives encouragement for numerous experiments in this direction. The hardened tissues may offer too much resistance to the delicate germ tubes of the sporidia, he says, which bore directly through the epidermis instead of entering through the stomata, as do the germinating uredospores and aecidiospores.

The behavior of the germinating teleutospores is influenced somewhat by their environment. MAGNUS (**23**) found that teleutospores of *P. graminis* kept under a thin layer of water formed a germ tube instead of a promycelium. These results were afterward confirmed by BLACKMAN (**5**), who also included two other genera. Other factors are sometimes operative, as KIENITZ-GERLOFF (**18**) reports that thin-walled teleutospores of *Gymnosporangium clavariaeforme* also form a germ tube. When teleutospores germinate in air, however, they almost invariably form sporidia. This is true of *P. graminis* even in Australia, where it has no aecidial host species.

The uredospores of *P. graminis* soon lose their viability, according to DE BARY (**3**), in one to two months if kept dry. BOLLEY (**6, 7**), however, obtained a germination of 5 per cent after exposing them to air and sunlight during the month of August, and even claims they may live over winter. Christman (**11**) failed to germinate them after November 23, although the uredospores of *P. coronata* were viable the 26th of January, and those of *P. rubigovera* the 21st of March. Perhaps the most extensive experiments of this kind have been made by ERIKSSON and HENNING (**16**), whose results show that the uredospores of both *P. graminis* and *P. glumarum* are unable to survive the winter in Sweden. The absence of fresh uredo pustules during two or three months in the spring is cited as additional proof, since the period of incubation after inoculation with uredospores is only about ten days. The

statement is also made by KLEBAHN (**19**) that "in Germany *P. graminis* does not appear to pass the winter as uredo." CARLETON (**9**) found this to be true in Kansas, and in a two weeks' trip through Texas in December 1895, he could find no rust on winter wheat or oats, although it was present there in abundance the previous summer.

The mycelium of the rust is not limited to the leaves and culms of cereals, but also enters the seed. ERIKSSON (**14, 16**) found it in abundance in the "peripheral tissues" of grains, but was unable to trace it into the young seedlings. ZUKAL (**34**) has made similar discoveries, and even found it in the seed coats of barley which was furnished by ERIKSSON and supposed to contain mycoplasm.

Spores of the Uredineae are frequently present in the seed of the host. SMITH (**30**) found teleutospores of *P. graminis* in oat grains lying next to the gluten layer, and ERIKSSON and HENNING (**16**) report the presence of both uredospores and teleutospores of *P. glumarum* in the pericarp of cereal grains.

Several rusts have been shown to infect their host species through the seed. CARLETON (**10**) demonstrated this conclusively for the *Euphorbia* rust (*Uromyces euphorbiae* C and P) with the seeds of *Euphorbia dentata*. The plants grown from disinfected seed were always free from rust, while the controls were heavily infected, although planted in sterilized soil and protected by bell jars. MASSEE (**25**) states that *P. malvacearum* Mont. commonly enters young hollyhock plants through the seed. According to MCALPINE (**26**) *P. beckmanniae* was introduced into Australia in 1903 and *P. impatientis* in 1904 through seed of *Beckmannia erucaeformis* and *Elymus condensatus*, respectively, received from the U.S. Department of Agriculture.

Experimental evidence seems to indicate that rusts may infect cereals through the seed. When oats were introduced into Ecuador by growing European seed in the botanical garden at Quito, LAGERHEIM (**21**) reports that the plants became heavily infected with *P. coronifera*, although neither this rust nor any of its aecidial hosts had ever been found in Ecuador. Carefully planned experiments, covering a period of years, were conducted by ERIKSSON (**15**) to determine whether *P. glumarum* winters in the seed of wheat

and barley. Glass cages of various sizes and types, provided with cotton ventilators to filter the air and caps to keep out the rain, were employed. Some were attached to a suction pump and artificially ventilated; others, on all sides except the north, were fitted with double panes of glass, between which was passed a continuous current of water. Despite all these efforts to produce a normal environment for the plants, the air inside the cages was always 2–6° degrees hotter than the air outside, and the light considerably diminished. The plants were always abnormal, often attaining two or three times the height of their outside neighbors. In a few cases a single winter cereal plant was placed in each of several glass tubes early in the spring, long before any rust appeared outside. As a rule, however, seeds were planted in pots of sterilized soil and placed in the bottom of the cages. As all the air entering the cages passed through cotton filters, no spores could be carried in from the outside. Although the majority of his results were negative, a considerable number of infections was obtained with both winter cereals and annuals. This he considered fully as much as could be expected, since the plants were grown under abnormal conditions. A similar set of experiments was planned by MASSEE (**25**), who planted wheat seed infected with *P. rubigo-vera* in two pots of soil and kept them covered with bell jars provided with cotton wool filters. In one pot 26 per cent of the plants rusted, and in the other 47 per cent, while not a pustule appeared on the controls.

The amount of rust developing in the grain field seems to vary somewhat with the date of sowing. Both the early and late grain, according to ERIKSSON and HENNING'S tables for the different cereals, are usually less rusty than those sown at an intermediate date. GALLOWAY (**17**) called attention to this fact in 1893, when all his duplicate plots of grain, sowed ten days later than the originals, were free from rust. Moreover, he says, "Examining the weather records for ten days preceding the rust, we find nothing to warrant the belief that the simultaneous appearance of the fungus the first week in May in widely separated spots was due to peculiar climatic conditions."

ERIKSSON'S well known mycoplasm theory was advanced to

explain such cases. This theory is based chiefly upon the claim that rust apparently infects the cereal host through the seed, although its mycelium is not recognizable in the germ by aid of the microscope and present cytological technique. KLEBAHN (**20**), for a time at least, supported this view, and even figured the nuclei of the fungus while in the mycoplasmic condition.

The following experiments on the life history of *P. graminis* were made at the North Dakota Agricultural College and Experiment Station at Fargo, North Dakota, to obtain information which would aid in producing a rust epidemic yearly in our wheat breeding plots to test the strains selected for rust resistance. This is a spring wheat region, where the winters are exceedingly cold and consequently winter cereals are not grown.

The germinating rusted wheat grains were studied at Madison, Wisconsin, under the direction of Dr. R. A. HARPER.

## Method

All the plants used for inoculation, except when otherwise stated, were grown in the greenhouse in beds containing 6–8 inches of fertile soil. The grass plants were transplanted to pots and placed in the greenhouse several weeks before they were used. The temperature was kept reasonably cool, and the air fairly moist by frequently watering the floor.

The inoculations were made by first mixing the spores of a pustule in a small quantity of distilled water. The plants were then moistened with distilled water by means of an atomizer and the spores applied with a camel's hair brush. Except in a few cases where the plants were very large, they were kept under bell jars 24–48 hours. If they became dry, they were sprayed again the second day. Generally, however, they were quite moist when the covers were removed. For part of the work inverted test tubes attached to stakes at suitable heights were employed, the lower end being lightly closed with cotton wool. The test tubes were found to retain the moisture even better than the bell jars. Parallel marks were sometimes made on the leaves by means of India ink and the spores placed between them. The

beds containing these plants were generally watered just before making the inoculations, to provide a source of moisture for the air beneath the covers. When not stated, the height of the plants on which bell jars or test tubes were used varied from 8 to 13 inches, without straightening up the leaves.

The wheat seedlings, grown from the rusted seed at Madison, Wis., and sectioned for study, were killed and fixed in Flemming's strong solution, imbedded in paraffin, and stained with either iron-alum hematoxylin or the triple stain.

## Experimental investigations

Experiments were begun to show how readily sporidia of *P. graminis* from wheat and native grasses infect the barberry, although there are very few barberry bushes in North Dakota, so few in fact that they could hardly be considered as a source of rust epidemics, unless miraculous powers were attributed to the wind in causing a widespread and uniform distribution of aecidiospores. In the following experiments small pieces of dead straw, which were covered with teleutospores of *P. graminis* and had lain on the ground during the winter, were arranged parallel to each other and tied longitudinally on the branches of the barberry bushes (*Berberis vulgaris*), just as the buds were beginning to unfold in the spring.

TABLE I

INOCULATION EXPERIMENTS WITH TELEUTOSPORES OF *Puccinia graminis* Pers.

| Number of experiment | Date of inoculation | Source of material | Number of branches inoculated | Results |
|---|---|---|---|---|
| 5 | April 30, 1906 | Agr. ten.* | 5 | 5 positive |
| 6 | April 30, 1906 | Agr. ten. | 7 | 1 positive |
| 7 | April 30, 1906 | Wheat | 2 | 2 positive |
| 9 | April 30, 1906 | Agr. rep. | 2 | 2 positive |
| 10 | April 30, 1906 | Wheat | 1 | 1 positive |
| 11 | April 30, 1906 | Hord. jub. | 2 | 2 positive |
| 12 | April 30, 1906 | Ely. trit. | 2 | 1 positive |
| 13 | April 30, 1906 | Wheat | 1 | 1 positive |
| 14 | May 2, 1906 | Wheat | 3 | 3 negative |

* Abbreviations: Agr. ten. = *Agropyron tenerum;* Agr. rep. = *Agropyron repens;* Hord. jub. = *Hordeum jubatum;* Ely. trit. = *Elymus triticoides;* Ber. vul. = *Berberis vulgaris.*

In experiments 5–13 inclusive, the inoculated barberry branches were heavily infected the 14th of May. Only spermagonia were present on this date, but they were frequently on both surfaces of the leaves. There were a few spermagonia on other parts of the bushes, but no such dense blotches as appeared where the rusty straw was applied.

Further inoculations were made upon the barberry by scraping the teleutospores from dead straw, wintered the same as that described for Table I, and placing it on young buds or leaves which were carefully marked off by India ink and tagged. These results are recorded in the following table.

TABLE II

INOCULATIONS MADE UPON *Berberis vulgaris* WITH TELEUTOSPORES FROM *Puccinia graminis* Pers.

| Number of experiment | Date of inoculation | Source of material | Number of parts inoculated | Results |
|---|---|---|---|---|
| 19 | May 8, 1906 | Oats | 10 buds | 10 negative |
| 22 | May 9, 1906 | Ely. trit. | 10 buds | 2 positive |
| 27 | May 21, 1906 | Ber. vul. | 10 buds | 10 negative |
| 28 | May 22, 1906 | Wheat | 8 leaves | 8 positive |
| 52 | June 26, 1906 | Ely. trit. | 1 leaf | negative |
| 53 | June 26, 1906 | Hord. jub. | 1 leaf | negative |

As shown by the table, these results were mainly negative, perhaps on account of poor germination, since the buds selected were fully as young as those used earlier.

In order to obtain pure cultures of aecidiospores of known origin for further experiments relative to their infecting power, inoculations were made upon barberry bushes which had been standing in the greenhouse in large tubs for nearly a year and had borne no rust. The infections were made by tying small pieces of old rusty straw on the bushes in places offering the least opportunity for contamination and moistening the straw frequently with distilled water. A summary of the results is shown in Table III.

Aecidia appeared only on parts of the barberry inoculated, and, with the exception of the rusty oat straw from which all my inoculations so far have failed, infections were obtained from each kind of material. This with the data of the two preceding

tables shows that under favorable conditions *P. graminis* passes readily to the barberry from wheat and certain grasses, viz., *Agropyron tenerum*, *A. repens*, *Hordeum jubatum*, and *Elymus triticoides*, confirming the general results of DE BARY and others.

TABLE III

INOCULATIONS MADE UPON *Berberis vulgaris* WITH TELEUTOSPORES OF *Puccinia graminis* Pers.

| Number of experiment | Date of inoculation | Source of material | Method | Results |
|---|---|---|---|---|
| 1 | March 29, 1907 | Agr. ten. | Bell jar | Positive |
| 2 | March 29, 1907 | Agr. ten | Bell jar | Negative |
| 3 | March 29, 1907 | Agr. rep. | Bell jar | Positive |
| 4 | March 29, 1907 | Agr. rep. | Bell jar | Negative |
| 5 | March 29, 1907 | Oats | Bell jar | Negative |
| 6 | March 29, 1907 | Oats | Bell jar | Negative |
| 7 | March 29, 1907 | Oats | Bell jar | Negative |
| 8 | March 30, 1907 | Wheat | Bell jar | Positive |
| 9 | March 30, 1907 | Wheat | Uncovered | Negative |
| 10 | March 30, 1907 | Hord. jub. | Bell jar | Positive |
| 11 | March 30, 1907 | Hord. jub. | Uncovered | Negative |
| 12 | April 4, 1907 | Wheat | Uncovered | Negative |
| 13 | April 4, 1907 | Wheat | Uncovered | Negative |

Observations were made on the dissemination of rust from barberry bushes by taking note of the infection on the surrounding grasses. There was a small barberry hedge in Fargo very favorably located for this purpose, as it was surrounded on three sides by meadow and was heavily rusted every year. Careful observations for three successive springs (1905–1907) furnished some surprising data. Early each year, the plants of *Hordeum jubatum*, *Agropyron repens*, and *A. tenerum* in the immediate vicinity of the hedge became thoroughly covered with the uredo stage, while *Phleum pratense* and *Poa serotina* were absolutely free from it, and *Elymus virginicus* bore only an occasional pustule. The rust was abundant within 25 yards of the barberry bushes, but practically disappeared at a distance of 60 yards. The most persistent searching was required to discover a single pustule beyond 80 yards, and in no one of the three springs at this early date, before rust had begun to spread from the uredospores, could I find fresh uredo pustules of *P. graminis* beyond 100 yards from the barberry hedge, notwithstanding the fact that in 1905 rust was fairly abun-

dant in this region. Either the aecidiospores are not borne as great distances by the wind as formerly supposed, or their germinative power is remarkably low. There is some additional evidence in support of the latter view.

Plots of small wheat plants in the experimental garden were sprayed repeatedly with aecidiospores in the spring of 1905, yet scarcely any rust appeared until the plants were nearly two feet high, a fact commonly observed here in the field every spring, although volunteer wheat plants barely out of the ground in the fall are often covered with rust.

Two series of infection experiments were made to obtain further data with reference to the spreading of *P. graminis* by means of its aecidiospores. From 98 aecidial pustules, taken at random in 1906, a total of 368 plants were inoculated. Plants of wheat, rye, oats, barley, and usually *Avena fatua*, *Agropyron tenerum*, *A. repens*, and *Hordeum jubatum* were inoculated from each aecidial pustule and covered with bell jars 24–48 hours. Germination tests of the spores, made by placing them in water and on wet filter paper kept in a moist chamber at 18–20° C., showed a viability of about 8 per cent. Rust appeared only on *Avena fatua*, *Agropyron repens*, rye, oats, and *Hordeum jubatum*. No plants of barley or wheat were infected. These experiments were repeated in 1907 by inoculating 247 plants from 13 pustules of known origin, the original host species always being included in each group. Tests of the spores showed about the same percentage of germination as those used in the former experiments. No barley plants were infected, and the only wheat plants which developed rust were those inoculated with a form which came originally from wheat. The aecidiospores of only 9 pustules, however, of the 111 used in the two series of experiments caused infection. This relatively low number of infections agrees with the results obtained by repeatedly spraying the wheat plots with aecidiospores in 1905, and may partly account for the confining of the rust to the immediate vicinity of the barberry hedge as observed for the three successive years 1905–1907. It is also in harmony with the very limited spreading observed by both MARSHALL and SCHÖLER when they set barberry bushes in the

grain fields, and might easily be accounted for by the change of host species if the heteroecism of the fungus is only facultative.

A suspicion has frequently been expressed that the black rust spreads to the grain fields by aid of the grasses which either harbor the mycelium over winter or are infected early by aecidiospores. In order to determine the interval between the appearance of rust on grasses and cereals, the following observations were made in the spring of 1905. Rust the following summer, although not as abundant in North Dakota as in 1904, was still quite pronounced.

TABLE IV

FIRST APPEARANCE OF *Puccinia graminis* Pers. UPON GRASSES AND CEREALS AT FARGO, NORTH DAKOTA, IN THE SPRING OF 1905

| Date of observation | Host species | Spore pustules | Location | Remarks |
|---|---|---|---|---|
| June 27 | Hord. jub. | Uredo | Grass garden | A few pustules on a single plant |
| June 29 | Hord. jub. | Uredo | Near barberry | |
| July 6 | Spring wheat | Uredo | Field | Far removed from barberry bushes. |
| July 9 | Agr. rep. | Uredo | Near barberry | Present in abundance on both Agr. rep. and Hord. jub. None found elsewhere although a diligent search was made. |
| July 10 | Winter wheat* | Uredo | Field | Found in abundance at a considerable distance from barberry bushes. |
| July 12 | Agr. rep. | Teleuto | Near barberry | Present on both Agr. rep. and Hord. jub. |
| July 13 | Winter wheat | Teleuto | Field | Same plot of winter wheat mentioned above. |
| July 16 | Spring wheat | Uredo | Field | Appearing quite generally on all the oldest wheat. |

* This was an experimental plot of winter wheat in charge of Dean J. H. SHEPPERD, the agronomist, and the writer was not aware of its presence until July 10, when the plants which had survived the winter were thoroughly covered with mature uredo pustules of *P. graminis*, some quite old, the rust having first appeared probably 10–14 days earlier.

The foregoing table shows that *P. graminis* probably appeared upon the experimental plot of winter wheat almost or quite as early as upon *Agropyron repens* and *Hordeum jubatum*, even when the latter were in the immediate vicinity of the barberry. It also shows that, with the exception of the one case mentioned

under date of June 27, the uredospores of *P. graminis* were generally present upon the spring wheat earlier than they were observed upon the wild grasses remote from the barberry bushes. In fact, *P. graminis* was present in the uredo stage upon spring wheat July 6, and with one exception could not be found upon the grasses remote from the barberry even July 9, after which date no further search was made for uredo upon the latter.

Experiments were made to obtain data with reference to the spread of *P. graminis* from grasses to the wheat fields by means of the uredospores. Twenty-eight uredo pustules were selected from *Agropyron tenerum*, *A. repens*, *Avena fatua*, and *Hordeum jubatum*, and 230 plants inoculated. From each pustule inoculations were made upon plants of wheat, barley, rye, and oats, and upon the host species from which the rust was obtained. Parallel marks were made upon the leaves with India ink, and the spores placed between them in order to distinguish the results of regular inoculations from accidental infection. There was very little spreading of the rust, however, as the infected leaves were always removed from the greenhouse. The plants were covered with bell jars 24–48 hours, as formerly. Germination tests of the uredospores showed an average viability of 70–80 per cent.

The uredospores of 21 of the 28 pustules caused infection, but showed a decided preference for certain host species. The rust readily infected rye, oats, and the grasses, but not wheat or barley. In fact, the results of the few experiments made seem to show what was anticipated from the two series of infection experiments with aecidiospores, viz., that one form of *P. graminis* is common to *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, *Avena fatua*, oats, and rye, but is incapable of infecting either barley or wheat. This furnishes little encouragement to those who believe that *P. graminis* is spread to the wheat fields from the barberry bushes or from occasional protected spots, as beneath ice by aid of the native grasses. The data however give no information with respect to the forms of *P. graminis* on wheat or barley, as neither was infected, but in our breeding experiments in 1905 a number of wheat plots were surrounded by a border of barley which was practically destroyed by black rust, and yet there was no visible

evidence that it ever spread to the wheat. Hence it appears that the forms upon these two species are distinct.

The wintering of *P. graminis* as mycelium in plant tissues in North Dakota is extremely doubtful, as there are no winter cereals and the uredo stage does not appear upon the grasses until very late in the spring, when they are quite large. To test the supposition, however, that the fungus might pass the winter in occasional plants under shelter and produce a new outbreak of uredo the following season, I placed heavily rusted plants of *Agropyron tenerum*, *A. repens*, *Hordeum jubatum*, *Elymus virginicus*, and *E. canadensis* in large pots three successive falls (1904–1907) and transferred them to the greenhouse where they remained until summer, but no fresh uredo pustules ever appeared on any of them. Furthermore, in collecting data relative to the appearance of *P. graminis* upon cereals and grasses in the spring of 1905, a piece of low meadow containing *Hordeum jubatum*, *Agropyron tenerum*, and *A. repens*, which was flooded by the city in the winter and used as a skating pond, was carefully observed, but no uredo pustules appeared here until they were found on the grains and grasses elsewhere.

The origin of spring infections has frequently been attributed to over-wintered uredospores, although this is merely a hypothesis. In order to determine with some accuracy the duration of the germinative capacity of the uredospores of *P. graminis*, the following experiments were made. Bundles of rusty straw which had stood in the shock until late in the fall of 1904 were placed on the ground. Others were tied to trunks of trees, and some stored in the attic of one of the college buildings, where the temperature was below freezing but much warmer than the outside atmosphere. Rusty wheat straw was also put in manila envelopes and in test tubes, and these laid in pasteboard boxes on the ground. All the material placed upon the ground was covered by snow the greater part of the winter. To still vary the conditions, test tubes of rusty wheat straw were attached in an inverted position to stakes outside, 2–3 feet above the ground, while packets were buried in ice at the ice house and others kept in the laboratory. From the middle of September to the following July germination tests of the uredospores were made once a week from all these sources. At

the beginning of the experiment, about 10 per cent of the uredospores were viable, but by the end of September this had dwindled to 2 per cent; and only an occasional uredospore germinated in October and none whatever after November 15.

Some confusion arose at first over a fungus whose hyphae emerged from the germ pores, but without showing any conspicuous evidence of its entrance. This fungus proved to be an *Alternaria*, which parasitized many uredospores.

Repeated attempts were made to germinate uredospores from *Hordeum jubatum* and occasionally from *Agropyron repens* which were buried under ice and snow, but always without success. Old uredospores can be obtained in abundance all winter and in early spring on *Hordeum jubatum*, lying between the stem and sheath, but it is practically impossible to find them here on other grasses in winter, although the plants may be buried under ice in low places, as they drop off before winter and are replaced by teleutospores. Hence no uredo pustules were available from other grasses except *Agropyron repens*, whose few winter-borne uredospores would not germinate.

The germination tests show that during the winter of 1904–1905 in North Dakota all or practically all the uredospores of *P. graminis* probably lost their viability, and hence were not the cause of the large amount of black rust in the state the following summer.

The annual reappearance of *P. graminis* in Kansas, Nebraska, and the Dakotas has often been explained by assuming that it passes the winter in Texas and spreads north by means of the wind and growing crops. To obtain data on this point an endeavor was made to catch uredospores of *P. graminis* from the air before any pustules appeared upon the wheat. A post 5 feet high was set in the edge of a wheat plot and a soup dish 7 inches in diameter, containing a small quantity of distilled water, just enough to fill one tube of the centrifuge, was exposed at its top 30–40 minutes. The whole inner surface of the dish was rinsed with the water to collect any spores adhering to its sides. The water was then poured into a tube provided with a tapering bottom, and the débris precipitated by means of a centrifuge. All the particle-bearing liquid was removed from the narrow end of the tube by

means of a pipette, placed upon six slides and examined microscopically. This process was repeated two or three times a week for nearly a month, but no uredospores of *P. graminis* were caught until uredo pustules were abundant on the surrounding wheat.

Further observations were made to determine whether uredospores are commonly borne very great distances by the wind. On a piece of ground one-third to one-half acre in area, which we used for breeding rust-resistant wheat, a rust epidemic was produced every year. This was accomplished by plowing into the soil rusty wheat straw and spraying the wheat repeatedly with aecidiospores of *P. graminis tritici* Erik. and Henn. It should also be mentioned that our original seed, the foundation stock, was obtained from the badly rusted crop of 1904. Hence there were present teleutospores, aecidiospores, uredospores, and probably infected seed. For the present, however, we are concerned only with the fact that rust annually appeared upon these plots in great abundance. In fact it was almost impossible to obtain any plump kernels of wheat from plants grown here. During at least two summers (1906–1907), when these plots were thoroughly covered with *P. graminis*, there was scarcely any rust on the field plots of wheat which lay a short distance north of the infested area and in the direction of the prevailing winds, although the latter passed over the breeding plots, often causing considerable annoyance while I was taking rust notes. The only possible hindrance to the passage of the spores was a few rows of shrubs covering a strip about 10 feet wide, thinly planted and varying from 6 to 8 feet in height, located 20–25 yards from the rust bed. However, there was a road about 20 feet wide running north and south through the shrubbery and along the west edge of the infested area. Hence there was ample opportunity for wind distribution of the uredospores, and former experiments have shown that they were highly viable during the summer of 1906, yet practically no rust appeared upon these neighboring wheat plots. The fact that *P. graminis* does not appear upon wheat in North Dakota in the summer until the plants are nearly 2 feet high, several weeks after the wheat crop is harvested in Kansas and Nebraska,

would also appear to indicate that the spores are not commonly borne very great distances by the wind.

Little or nothing has been done in the past to test the possible infection of sprouting cereals by means of germinating teleutospores from the soil. When buried in moist earth it is not even known whether teleutospores can produce germ tubes or promycelia. A striking fact in connection with the possible infection of seedlings by teleutospores was observed in our field work. Our breeding ground, in which we produced an abundance of rust annually as described above, consisted in 1907 of three parts which, however, were not separated by paths or any visible marks. The whole west half had grown three successive crops of rusted wheat (1905–1907); all the east half except a narrow strip on the north end grew rusted wheat in 1905 and 1907, but produced a crop of flax in 1906; the remainder was in sod until 1907, when it was planted to wheat. The rusty wheat instead of being removed from the ground was always plowed under. The same varieties, except some of Farrer's wheat which was not taken into account, were planted on all three areas at the same dates. The soil was equally level and very fertile. All the wheat was inoculated alike during the spring and summer of 1907, yet shortly before harvest the three parts were separated quite distinctly by lines of rust demarkation, the amount of rust varying with the number of crops of rusted wheat grown upon each area. Whether these results are due to the different quantities of teleutospores in the soil of the different areas or not cannot of course be definitely stated, but they are at least suggestive of the need of further experiments in this direction. If the perpetuation of the wheat rust in the absence of the barberry is due to the teleutospore infection of the germinating seed, variation in the time of seeding might easily account for the annual variability in its prevalence.

The further possibility that rust may be carried in the seed itself is certainly also to be considered. Teleutospores and mycelial fragments of *P. graminis* are often present in abundance in the pericarp of wheat grains, and can frequently be recognized by the appearance of pustules, as will be described later. Early in the spring of 1905 about 60 wheat grains with such contamination

were planted under each of two glass cages provided with cotton ventilators to prevent the entrance of spores from the air. The experiment was afterward repeated in the greenhouse, but rust never appeared on the plants in either case. The conditions however were exceedingly abnormal. The ventilators were entirely too small and the moisture inside the cages was always excessive. While the plants grew rapidly, headed, and blossomed, they failed to set seed both years. Another experiment made in the spring of 1905 appeared to give more favorable results. Wheat was sowed at various dates, some of it quite late. It was all inoculated early and repeatedly with both aecidiospores and uredospores of *P. graminis tritici* Erik. and Henn., the latter being obtained chiefly from the experimental plot of winter wheat of the same source as noted above, but the wheat of every sowing remained nearly free from rust until it began to head, when each in turn became thoroughly rusted. It might be assumed on this evidence that wheat has only a definitely limited period of susceptibility, still very small volunteer wheat plants are often quite rusty in the fall. It is possible to attribute this peculiar behavior to infection through the seed with a long subsequent incubation period in the growing plant, although the possibility of its coming through the soil is not excluded.

The infection of wheat grains with *P. graminis* can often be recognized by the presence of a tiny black spot where the grain separated from the mother plant. When black, this area is generally filled with teleutospores, which can be distinguished in mass with the naked eye or at least with the aid of a hand lens. Such grains are usually shrivelled, but occasionally they remain quite plump. Grains showing a spot of larger area with somewhat irregular boundaries are usually infected with other fungi, as *Alternaria* or *Helminthosporium*, and may not even contain rust. These are the so-called "black-points" mentioned by BOLLEY.[4]

In rusted grains of wheat the pustules are usually most abundant in the thick portion that was formerly attached to the rachilla, but they are also found in other parts of the pericarp, and often lie in the seed coats where they are pressed against the endosperm

[4] Science, Oct. 21, 1910, p. 1.

or embryo. As many as 10 pustules are sometimes seen in a single section, and nearly all of them are wholly inclosed by the tissues. All about the pustules are masses of rust mycelium, but the hyphae are not confined to these areas. They extend considerable distances from the pustules, and are present in numerous grains in which teleutospores cannot be found.

To obtain further information relative to infection through the seed, badly rusted grains of wheat after germinating from one day to two weeks were studied in the botanical laboratory at Madison, Wis., by means of cytological methods. The seed available was a remnant of former experiments, 4 or 5 years old, and revealed some very interesting phenomena.

Teleutospores in certain pustules, lying in the region of the hilum, were found to be undergoing remarkable changes, resembling the so-called palmella formations of certain filamentous algae. The protoplasts appeared to grow and divide in various directions, often distending the walls until they became quite thin (figs. 5–13). The nuclei, though not well fixed, were present as irregular densely stained bodies. Frequently one or both cells of the teleutospore were still undivided (figs. 1–3, 15), but numerous later stages were present, in which the protoplast had divided one to several times. As a rule, the wall between the two original cells was quite thin and persisted for some time (figs. 5, 6, 8), but occasionally it could not be distinguished (fig. 7). In the latest stages observed the cells became more distinct, often rounding slightly and acquiring thicker walls (figs. 7, 8, 11, 12). A view of the apical end of the teleutospore represented by fig. 12 is shown in a lower focus in fig. 11. In numerous cases the two halves of the former teleutospore finally separated from each other, forming two more or less globular multicellular aggregates (figs. 13*a*, 18). That these conditions are due to a parasitic mycelium, which has penetrated the teleutospores and completely replaced the protoplasts of the rust, is of course a possibility to be reckoned with. As is seen from the figures, however, direct evidence of the presence of such a parasite is entirely lacking. There is no mycelium outside the rust cells, and no evidence of a gradual absorption and replacement of the rust protoplast by that of a parasite. The subsequent

behavior of the cells will of course show their true nature, but as material is not available for following them through the later stages of germination of the seedling, it seems best to publish as a preliminary account the figures of the stages already found. The importance of their bearing on a possible method of wintering of wheat rust in the absence of the barberry or uredo is apparent.

These peculiar phenomena were not confined to the teleutospores, but were frequently present in the stalk cells (figs. 2, 5, 9, 10), and even in the mycelial region below (figs. 14, 15). Fig. 14 represents a radial section through the base of a pustule, one teleutospore and neighboring stalk cells being included. As is seen, the growing cells of the sorus were associated more or less in groups, but usually interspersed with smaller empty cells. Sometimes they formed dense areas, where it was difficult to determine whether they were of hyphal or teleutosporic origin. Now and then faint outlines resembling distorted, multicellular teleutospores were seen in the mass, but in all probability at least some of the cells arose from the mycelium. Apparently identical cells were found in other parts of the pericarp remote from the pustules (fig. 17). Lying near were filaments composed of similar though usually smaller cells (figs. 16, 17, 19). These however were enlarged portions of a smaller mycelium, all the remaining cells being empty.

Quite separate from the cells just described, fragments and often considerable pieces of what appeared to be living rust mycelium were found mixed with dead hyphae of the rust (figs. 20–22). They were usually in the pericarp, but often lay next to the deepest layer. There were occasional places outside the region occupied by the layer of feeding cells where they passed through into the cells of the scutellum and were found in considerable abundance within 6 or 7 cells of the growing plant itself (fig. 21).

As noted, the fate of the teleutosporic and mycelial cells described above remains for future determination, as my present material contains no later stages. The evident suggestion is that they may serve as growing points for the development of new rust mycelia and the infection of the embryo and seedling.

The possibility for infection of the seedling when the pericarp

of the seed is filled with living rust would seem to depend chiefly on the presence of reserve food for the fungus and the capacity of the hyphae to grow through a few dead cells. The penetration of the dead tissue may and probably does offer some difficulty to the majority of the hyphae, but in some places only a single cell wall of the pericarp intervenes, which could scarcely be looked upon as an absolute obstruction. At any rate, an abundance of mycelium resembling rust was found in the scutellum close to the growing tissue, with apparently nothing to hinder its further progress in that direction.

Whether after infection of the embryo in the manner suggested the rust mycelium might grow with the plant and take on a virulent form at later stages, when it spreads to form pustules, is certainly an interesting possibility. Such a general systemic infection was assumed in ERIKSSON'S mycoplasm theory, and there is some evidence in the general behavior of the rusts as noted above to suggest such a possibility. That such a palmelloid growth of fungal hyphae under peculiar conditions of nutrition is to be expected is abundantly shown by RACIBORSKI'S interesting observation on a palmella-like growth of *Basidiobolus* when placed in media rich in nitrogen. Further investigation of the infection of wheat by rust through the seed will be made when suitable material is obtained.

## Summary

1. *Puccinia graminis* passed readily from wheat, *Agropyron tenerum*, *A. repens*, *Hordeum jubatum*, and *Elymus triticoides* to the barberry.

2. Observed facts seem to oppose the theory that aecidiospores and uredospores are carried considerable distances by the wind.

3. Uredo pustules of *P. graminis* appeared upon the experimental plot of winter wheat as early as upon grasses near the barberry bushes, and with one exception were generally present upon the spring wheat earlier than they appeared upon the grasses remote from the barberry.

4. *P. graminis* does not appear to spread to the wheat fields by aid of the grasses. The few experiments made seem to show three distinct biological forms of this fungus: one for wheat, one

for barley, and one for rye, oats, *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, and *Avena fatua*.

5. Uredospores of *P. graminis* failed to survive the winter of 1904–1905 at Fargo, North Dakota.

6. The wintering of *P. graminis* as mycelium in plant tissues in North Dakota is very doubtful, as shown by the late appearance of the uredo pustules in the spring and the failure of rusted grasses to produce the uredo again after being housed during the winter.

7. The pericarp of rusted wheat grains is frequently filled with rust mycelium and numerous pustules of teleutospores.

8. Teleutospores in some of the germinating grains appeared to be germinating in a palmella-like stage.

9. Pieces of mycelium resembling rust were found in the cells of the scutellum close to the growing plant.

In conclusion, I wish to acknowledge my indebtedness to Dr. R. A. HARPER for aid in the cytological study of the material and in the preparation of the paper.

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## EXPLANATION OF PLATE IV

Phenomena appearing in the mycelium and teleutospores of *Puccinia graminis* in rusted grains of wheat during germination:

FIGS. 1, 2.—Teleutospores, showing thin walls and cells preparing for division; fig. 2 also shows an enlarged distorted stalk cell in which a cell wall has been formed.

FIG. 3.—A teleutospore whose lower cell has divided.

FIGS. 4–6, 9, 10.—Early palmella-like stages, showing angular cells with thin walls.

FIGS. 7, 8, 11, 12.—Late palmella-like stages, in which the cells are more or less rounded, thicker walled, and less crowded.

FIG. 13.—A group of teleutospores lying in the edge of a pustule that was sectioned somewhat obliquely.

FIGS. 14, 15.—Radial sections through the base of pustules showing living cells of the sorus.

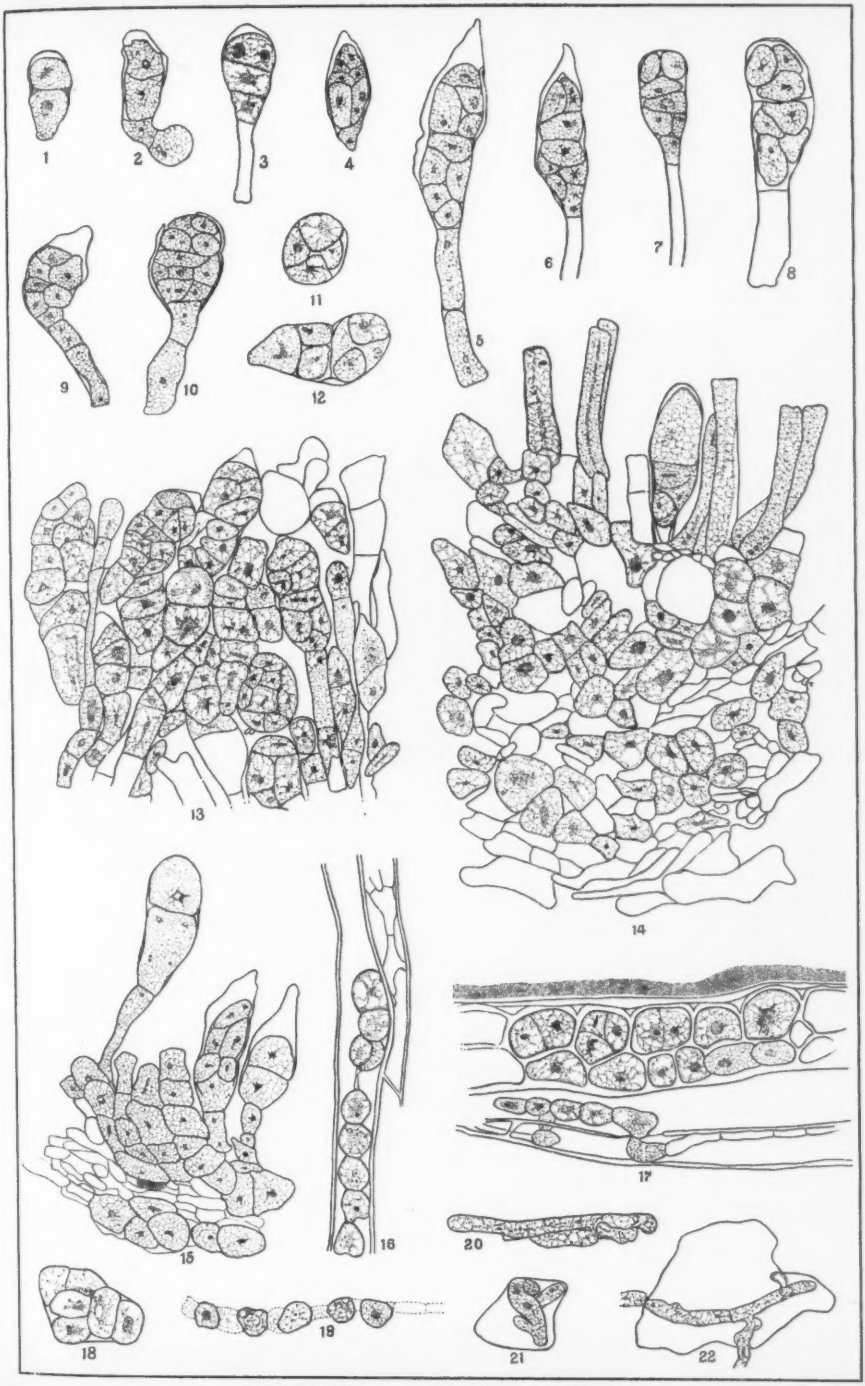
FIG. 16.—Mycelium lying in the pericarp; a few cells were alive and considerably enlarged, while the remainder of the filament was dead.

FIGS. 17, 19.—Dividing cells and living portions of mycelium lying in the pericarp remote from pustules; as in fig. 16, only a small portion of each filament was alive.

FIG. 18.—A group of cells found among the teleutospores of a pustule similar to that represented by fig. 13 (cf. 13*a*).

FIGS. 20, 22.—Fragments of mycelium found in the pericarp mixed with dead hyphae of the rust.

FIG. 21.—A typical piece of mycelium found in the scutellum within 6 and 7 cells of the radicle.




PRITCHARD on PUCCINIA GRAMINIS

# EVAPORATION AND PLANT SUCCESSION[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 147

GEORGE DAMON FULLER

(WITH SIX FIGURES)

The plant associations on the sand dunes of Lake Michigan have been described by COWLES (1), who has called attention to the succession which is here so strongly marked and so easily determined. In much of the region immediately south of the lake, the forest succession consists principally of associations dominated respectively by cottonwood, pine, black oak, white and red oak, and beech in the order named. These are usually designated the cottonwood, pine, and oak dunes, and the oak-hickory and beech-maple forests. They represent the major associations in a succession extending from the pioneer trees to the climax mesophytic forest formation of the region. The dynamic physiography and the details of the composition of the various stages in the succession have been so thoroughly discussed by COWLES that little further elucidation is necessary, but hitherto no attempt has been made to obtain any quantitative determination of any of the factors influencing this succession.

The researches of LIVINGSTON (2) and others have shown that the evaporating power of the air is a rather satisfactory summation of the atmospheric factors which determine the growth of plants during that portion of the season free from frost, and that it can be accurately measured by the porous-cup atmometer; accordingly, in the spring of 1910, a number of observation stations were established upon the sand dunes near Millers, Ind., and the rate of evaporation was determined during the ensuing growing season. Both the porous-cup atmometer devised by LIVINGSTON (3) and the type described by TRANSEAU (4) were employed in this investigation. They were mounted in wide-mouthed bottles having a

[1] A preliminary report of evaporation studies in the plant associations upon the sand dunes of Lake Michigan.

capacity of 500 cc., closed with tightly fitting cork stoppers that were perforated for the atmometer tubes and for bent capillary glass tubes which served to equalize the atmospheric pressure within the bottles with that of the exterior air, without causing any loss by evaporation or permitting rain water to enter the reservoir. The bottles were sunk in the soil about two-thirds of their height, so that the evaporating surface of the instruments was 20–25 cm. above the surface of the soil. Except where otherwise specified, the readings were made weekly by filling the bottles from a graduated burette to a file scratch on the neck. The small area of the water surface at this point made the probable error in readings less than $\pm 0.5$ cc., and this could have had no appreciable effect upon the results. The instruments were all standardized to the same unit before being used, restandardized at intervals of 6–8 weeks during the season, and a final correction made on their being collected in the autumn. By the coefficients thus obtained all readings were reduced to the standard adopted by LIVINGSTON (**5**) in his recent paper on the operation of the porous-cup atmometer. The directions given in that article were so closely followed that it is unnecessary to detail further the methods used in operating the instruments. Two or three atmometers were discarded during the season on account of various irregularities in their operation, but others either maintained a uniform rate of water-loss or showed a variation that progressed uniformly at a readily calculable rate. To provide still further against the possibility of serious error, two instruments were often maintained a few feet apart at the same station, and several stations were usually established in the same association, the mean of the various readings being taken as giving the true measure of the evaporating power of the air for that association.

No correction has been made for errors caused by rainfall, although during showers some water undoubtedly passes through the porous cup and into the reservoir, because it was thought that the amount of variation thus produced would be the same for all stations within so limited an area, and hence the comparative relation of results would remain unchanged. This assumption has been largely verified by BROWN (**6**), using an atmometer with a rain-

correcting valve. It is the intention of the writer, however, to employ this improved atmometer, also devised by LIVINGSTON (**7**), in the continuation of these studies.

Fifteen different stations were established in the various associations, care being taken to select spots which possessed the average amount of tree, shrub, and herbaceous vegetation characteristic of that specific association as a whole. Owing to a variety of accidents and other circumstances, all the stations did not give equally satisfactory and continuous records; hence the present preliminary report is confined almost entirely to the results from 10 stations in 4 different associations. Many of these records extend from May 6 to October 31, or over a period of 178 days; at other stations the record begins at a somewhat later date, but continues until the severe frosts of November 1, and includes the important part of the growing season for all except a few very early spring plants.

In order to facilitate comparisons between the various stations, and to exhibit the progress of the evaporation rate during the entire season, the average water-loss per day between the weekly readings has been calculated, and the results expressed in graphs with ordinates representing the number of cubic centimeters lost per day by a standard atmometer, the abscissae being the intervals between the weekly readings. The readings included within each calendar month are indicated at the top of the diagram. For convenience of reference, the stations are numbered consecutively, beginning with that nearest the lake shore.

The first group of stations was upon some slowly moving dunes directly north of the village of Millers, Ind., and between the southern shore of Lake Michigan and the Grand Calumet River. According to old maps, this river formerly discharged its waters into Lake Michigan very near the spot selected for one of these stations. Any such discharge has long since ceased, and its exact location has been entirely obscured by the advancing dunes, leaving the remaining river bed as a shallow channel in which the water has little or no current, the present discharge being some eight miles farther west. Dunes are now advancing into this channel at several points, and within a few years will doubtless occupy other portions

of its bed. Here, at a distance of 100 to 200 meters from the shore, the pioneer tree association becomes established, and persists upon dunes of variable size that are usually more or less actively moving. This association is characterized by a paucity of species, all having strongly xerophytic structures. *Populus deltoides*, *Salix glaucophylla*, *S. syrticola*, *Prunus pumila*, and the two grasses *Calamovilfa longifolia* and *Ammophila arenaria* are at this point the only conspicuous members of this rather open cottonwood dune association. In it, upon dunes that have become almost completely fixed, two stations were established on May 6, and a third on July 9, and at the three stations at least four instruments were maintained in constant operation until the last day of October. These stations were about 200 meters from the lake shore, some 100 meters apart, and about 12 meters above the level of the waters of Lake Michigan. At all stations the atmometers received a small amount of shade for a few hours of the day, and on account of the open nature of the association were little sheltered from the wind, the cups receiving a rather sharp sand blast during high winds. Station no. 1 had some sheltering groups of cottonwoods on a slight elevation of sand a few meters southeast of the instruments, and no. 3 possessed a similar but smaller shelter at the southwest. These differences of exposure to winds probably caused some of the variations in the records of the different stations, but affected very slightly the average rate for the season.

The graphs for three cottonwood dune stations have been plotted upon the same chart (fig. 1), and exhibit a great similarity in their general course and in their simultaneous maxima and minima. The rainfall at Chicago (20 miles distant) for the same period, expressed in centimeters, is shown for periods corresponding with those of the intervals between the evaporation readings, but as there seems to be no very exact correspondence between the amount of precipitation and the amount of evaporation, these data are omitted from the other charts. There is certainly a correspondence between the number of hours of cloudy or rainy weather and the amount of evaporation, but this has not been exactly determined, nor does it seem important in our present studies. The evaporation graphs indicate that the most critical period occurs

about the end of July, and this is also toward the end of a period of seven weeks with very little rainfall; hence it may be safe to assume, even without any direct data regarding soil-moisture, that

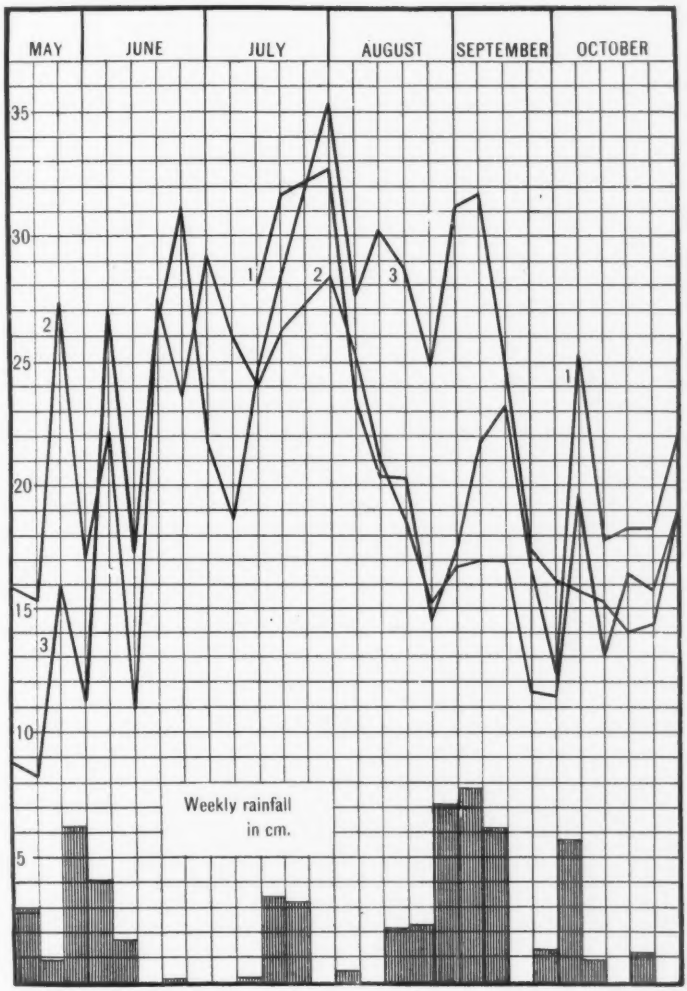



FIG. 1.—Evaporation rates in the cottonwood dune association at stations nos. 1, 2, and 3.

at this time there is a maximum demand by the atmosphere upon the water contained in the plant tissues, while at the same time only a minimum supply is available to replace such losses by transpiration. Two other periods of high evaporation are found to occur, one late in June and the other early in September. The latter is doubtless the one of greater stress, for it follows a month of very low rainfall. It will be seen that the maximum average evaporation for any week is just above 35 cc. per day, and that the minimum only once falls below 10 cc. per day. The average rate for the three stations upon the cottonwood dune for the 178 days of observation is 21.1 cc. per day.

The graphs (fig. 1) indicate that not only is the cottonwood dune an association with a very high rate of evaporation, but also that it is subject to excessive variation. This is most noticeable during May and June, but to a less marked extent prevails through the season, the fluctuations being decidedly greater than in the other associations (fig. 4). The mean of the readings of these three stations is believed to express most accurately the true measure of the evaporating power of the air during the growing season in the cottonwood dune association, and is therefore plotted and used in comparison with similar graphs from the other associations (fig. 4).

As the dunes gradually become fixed, an association dominated by evergreens succeeds the cottonwood dune. This pine dune association varies somewhat in composition in different localities, but in the area under consideration is dominated by *Pinus Banksiana*, associated with *Juniperus virginiana*, *J. communis*, and in the older portions containing also *Pinus Strobus*. In the undergrowth *Arctostaphylos Uva-ursi* is conspicuous, associated with *Rhus canadensis*, *R. toxicodendron*, *Prunus virginiana*, *Celastrus scandens*, seedlings of *Quercus velutina*, *Smilacina stellata*, *Asclepias tuberosa*, *Monarda punctata*, and other woody and herbaceous plants. Two stations were placed in this association at spots of medium density of growth about 100 meters south and east of the cottonwood dune series, but owing to several accidents only one record is worth reporting. This, from station no. 4, is unbroken for 178 days, and is often the mean of the readings from two atmometers.

This association is unique in the dominance of conifers, but is also notable for the comparative abundance of its undergrowth, although many species have decidedly xerophytic characters. That it is a comparatively short-lived association is evident from the presence of seedlings of *Quercus velutina*, the dominant tree of the succeeding association, very early in its history. Comparing the graph of its evaporation with that of the cottonwood dune (fig. 4), it will be seen that it is much lower, never reaching 20 cc. per day, and is subject to less violent fluctuations. Its maxima and minima are nearly synchronous with those of the cottonwood dune. The maximum evaporation rate is 17.5 cc. per day, the minumum falls below 4 cc., and the average for the season of 178 days is 11.3 cc. daily.

Proceeding inland from the lake shore, the pines gradually decrease in numbers, and the black oak, *Quercus velutina*, becomes more plentiful, until at a distance of about 500 meters south of the last station it forms an almost pure stand with only occasional trees of white oak, *Quercus alba*. The shrubby undergrowth consists principally of *Prunus virginiana*, *Rosa blanda*, *Viburnum acerifolium*, *Vaccinium pennsylvanicum*, *Ceanothus americanus*, and seedlings of *Quercus velutina* and *Q. alba*. Among the herbaceous members of the association are *Smilacina stellata*, *Lupinus perennis*, *Tephrosia virginiana*, *Lithospermum canescens*, *Asclepias tuberosa*, *Helianthemum canadense*, *Polygonella articulata*, and *Aster linariifolius*. In this oak dune association four stations were placed within a range of 100 meters; no. 6, on a fixed dune 15 meters high, well covered with the oak forest; no. 7, on a slope at an altitude of about 8 meters; and nos. 8 and 9, on the general floor of the forest some 5 meters above the level of the lake waters. All were about equally exposed and shaded. No. 6 was established on May 6, and the other stations on May 26. Station no. 9 was subject to so many interruptions that no report of its evaporation is presented, but the graphs from the other three (fig. 2) show a very close agreement, with differences corresponding directly to their elevation. A maximum of nearly 19 cc. per day occurred in May during the second week of the record, before the trees were in full foliage. The absence of leaves would largely account for this excessive rate,

but as it occurred when only one instrument was recording, it may be regarded as lacking confirmation, and as it could hardly be a critical period on account of the abundant water supply in the soil, it is disregarded in the general discussion. Throughout the remainder of the season the rate is rather high, but not subject to great fluctuations. A minimum of about 5 cc. per day is reached in September, and is followed by a distinct rise as defoliation pro-

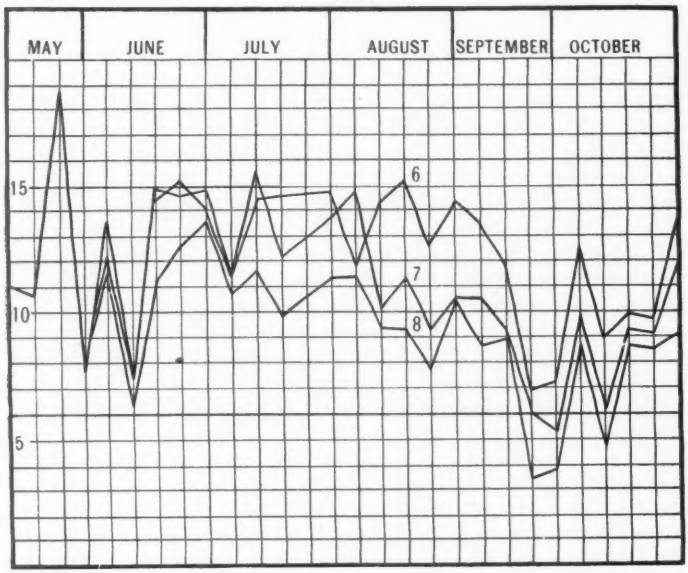



FIG. 2.—Evaporation rates in the oak dune association at stations nos. 6, 7, and 8.

gresses. Station no. 9 (not plotted) gives a somewhat higher rate during July, affording a maximum for that month and for the summer of 16 cc. per day. The average rate for the whole period is 10.3 cc. per day. The mean of all stations in the oak dunes is used (fig. 4) in comparison with similar graphs from the other associations.

At Millers, Ind., the vegetation exhibits no undisturbed successional stages beyond the oak dune, but 15 miles farther east, near the village of Otis, Ind., there is a tract of the climax deciduous

mesophytic forest dominated by the beech, *Fagus grandifolia*, and the maple, *Acer saccharum*. These two species form at least 85 per cent of the tree growth, with the remaining 15 per cent composed of *Tilia americana*, *Ostrya virginiana*, and *Prunus serotina*, and occasional trees of *Quercus rubra*, *Platanus occidentalis*, and *Liriodendron Tulipifera*. The undergrowth is largely seedlings of the dominant tree members of the association, together with *Cornus alternifolia*, *Viburnum pubescens*, *Asimina triloba*, *Sambucus racemosa*, and such herbaceous forms as *Trillium grandiflorum*, *Dicentra*

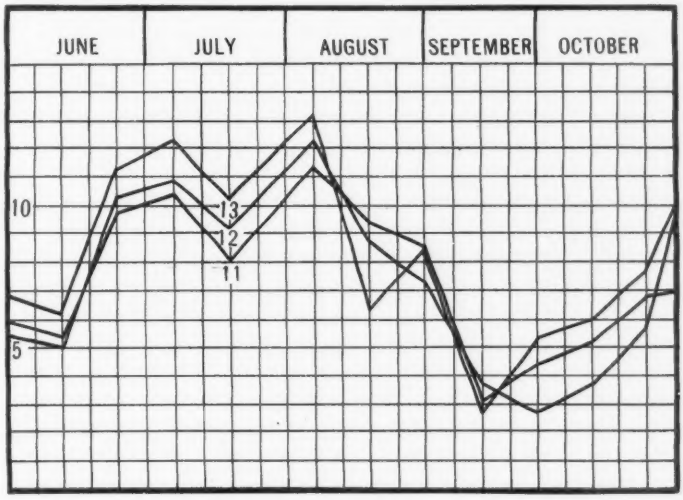



FIG. 3.—Evaporation rates in the beech-maple forest association at stations nos. 11, 12, and 13.

*canadensis*, *Adiantum pedatum*, *Asplenium angustifolium*, *Polystichum acrostichoides*, *Viola rostrata*, *Impatiens biflora*, *Erigenia bulbosa*, and *Epifagus virginiana*. As this represents the climax formation for a large portion of the United States, it was regarded as a standard to which other plant associations could be referred, and accordingly 3 stations were established in it on May 30, and maintained until the end of October, giving a continuous record for 155 days. On account of the difficulty in reaching these stations, readings were made only every second week throughout

the season. Of the 3 stations in the beech-maple forest, no. 11 was in an area dominated by the sugar maple and well surrounded by maple seedlings. No. 11 was near a large beech tree on a slope covered with *Asplenium angustifolium* and *Impatiens biflora*, while no. 13 was in the midst of beech seedlings between two large trees of the same species. Together they seemed to represent the average conditions in a beech-maple forest. The resulting graphs (fig. 3) are very similar, showing coincident maxima and minima differing but little in amount. The maxima are in July and August, and amount to little more than 12 cc. daily; the minimum occurs in September and is scarcely 3 cc. per day. The average rate of evaporation at the 3 stations for the 155 days is 8.1 cc. per day.

It is here interesting to note the close correspondence between the records for this beech-maple forest and those obtained by TRANSEAU (**8**) in a mesophytic forest containing a small percentage of beech and situated on Long Island, N.Y., where for the period of observation from June 5 to July 2, 1907, the evaporation rate averaged 8.5 cm. daily, compared with 8.4 cm. daily during the month of June, 1910, in the Otis, Ind., forest. While it is not safe to draw any very definite conclusions from records covering but a single month, it may be assumed that the two associations differ very little in the amount of mesophytism developed.

Several methods may be employed in comparing the data obtained from the various evaporation stations. Perhaps the best is to plot upon the same chart graphs representing the mean daily evaporation by weeks, from the several stations in the different associations (fig. 4). It will be seen that the graphs show several similarities, but more differences. The maxima and minima are generally coincident in time and proportionate in amount. All show great irregularity during spring and autumn, and a comparatively high rate during July and August. The general height of the different graphs probably gives the most instructive and interesting differences in the various habitats. That of the cottonwood dune is farthest removed from those of the other associations, and shows a habitat not only with great evaporating power, but one of great extremes, the difference in rate between

two consecutive weeks being nearly or quite 10 cc. per day during May and the first part of June, and on two occasions amounting to an increase of 100 per cent in one week as compared with the preceding. This occurring early during the growing period would doubtless be very unfavorable for the development of any seedlings, especially as it was followed by the very high rates of the succeed-

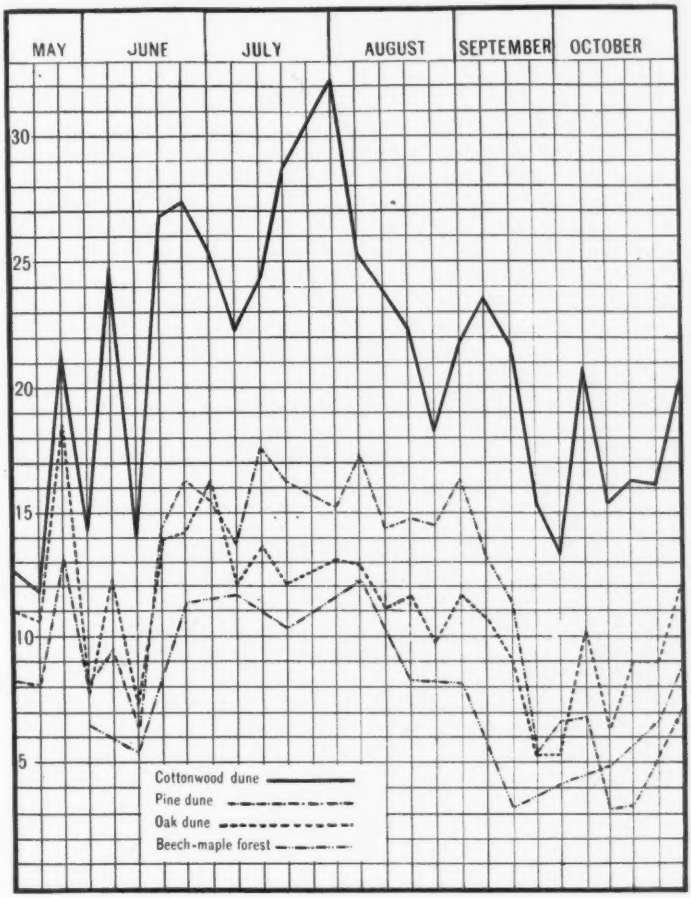



FIG. 4.—Mean daily evaporation rates in the sand dune plant associations and in the beech-maple forest.

ing months. The high maximum occurring at midsummer would probably prove the excluding factor for all mesophytic plants, even if not combined with such other factors as the deficiency of soil water at the same time. Such a graph seems to depict rather well a habitat of atmospheric extremes making large demands upon all available water, and naturally and necessarily resulting in a xerophytic plant association, with a very limited undergrowth and an almost entire absence of herbaceous plants and seedlings. Perhaps nowhere could an association be found so entirely dependent upon vegetative reproduction for its maintenance, for almost without exception any increase in vegetation is the result of subterranean branches.

The graph for the pine dunes is decidedly lower and more regular in its contour than that of the association which it succeeds. Its four nearly equal maxima would indicate that within its limits there was throughout the summer season a continuous stress rather than a series of violent extremes. On the whole, it shows a water-demand of little more than half of that occurring in the cottonwood dune. Its greatest divergence is plainly due to the evergreen character of its vegetation, and is seen in its low range in May and the first part of June, and again in October, when it falls below that of the oak dunes and is even less than that of the beech-maple forest. This would give good reasons for expecting to find within this association truly mesophytic plants, whose activities are limited to the early spring.

The graph from the oak dune stations shows two surprisingly high points; one during May, that may be partially explained by the absence of foliage; and the other near the end of June, which seems to coincide with maxima in the other associations. On the whole, it is more moderate during the months of summer than that of the pine dune, but the difference is not so great as to make it surprising that its undergrowth differs but little from that found in the pine dune association.

The graph from the beech-maple forest stations is one of moderate height and great regularity. It is but fair to say that weekly readings would probably have introduced some minor irregularities, but without changing its general course or influencing the

average rate for the season. At no point does it reach to half the height of that from the cottonwood dune, but surpasses that of the pine dune in October.

The data of these observations relate only to the stratum of vegetation immediately above the surface of the soil, and would be quite different at a height of one or two meters. This lower stratum, however, is the critical one for a forest association, for the development of tree seedlings occurs within its limits, and

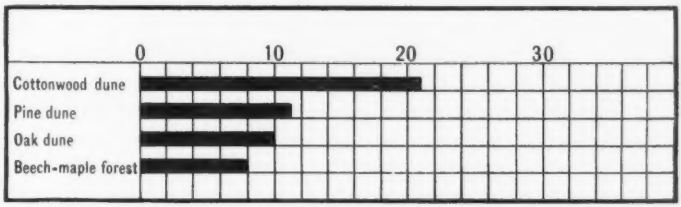



FIG. 5.—Diagram showing the comparative evaporation rates in different associations on the basis of the average daily amount from May 6 to October 31, 1910.

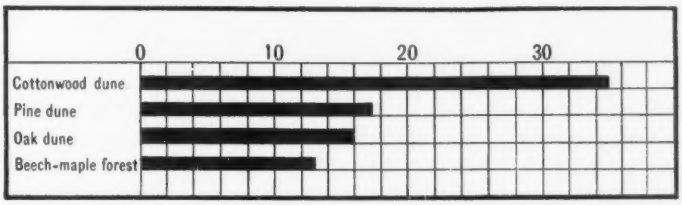



FIG. 6.—Diagram showing the comparative evaporation rates in different plant associations on the basis of the maximum average amount per day for any week between May 6 and October 31, 1910.

therefore it is the portion of the habitat which determines the forest succession and hence the most important ecologically. A single example may be cited from the meager data obtained during the past season regarding the rates of evaporation in the more elevated strata. Very near station no. 13 in the beech-maple forest, an instrument was established 2.5 meters above the surface of the soil, and showed for the season an average of 12.7 cc. daily, as compared with 9.1 cc. daily for no. 13, whose atmometer was 20 cm. above the surface.

The comparative rates of evaporation in the different plant associations may be compared in other ways. If the average amount of water lost by the standard atmometer daily throughout the season be taken as a basis and represented in a diagram giving the loss in cubic centimeters (fig. 5), a graphic representation results which, however, tells little more than what has been shown differently in fig. 4. Likewise, the maximum daily rates for the week of greatest evaporation during the season gives a similar representation of the conditions in the several plant associations (fig. 6). Upon a percentage basis, with the average rate per day throughout the season in the beech-maple forest taken as a unit, the comparative evaporation rate in the oak dune is 127 per cent, in the pine dune 140 per cent, and in the cottonwood dune 260 per cent. As the months of July and August probably represent the critical portion of the growing season with reference to its water supplies, a comparison like the preceding might be made for those months only, when it would be found that the comparative evaporation in the oak dune would be 113 per cent, in the pine dune 146 per cent, and in the cottonwood dune 230 per cent.

## Summary

1. These data represent the evaporation rates in the lower but critical stratum of the plant associations.

2. Evaporation at different stations in the same plant association exhibits variations similar in character and degree.

3. The rate of evaporation in the cottonwood dune association, both by its great amount and by its excessive variations, seems a sufficient cause for the xerophytic character of the vegetation and for the absence of undergrowth.

4. Evaporation in the pine dune association exceeds that in the oak and beech associations except when the latter are devoid of foliage.

5. The vernal vegetation of the pine dune is quite as mesophytic as that of the succeeding association, thus agreeing with its lower evaporation rate during that portion of the year.

6. Evaporation in the various associations varies directly with the order of their occurrence in the succession.

7. The differences in the rates of evaporation in the various plant associations studied are sufficient to indicate that the atmospheric conditions are efficient factors in causing succession.

## Conclusions

From the study of the data available, it seems evident that the porous-cup atmometer measures with very considerable accuracy the atmospheric factors which combine in making demands upon the water-supply of the aerial portion of the plant; the data, therefore, may be directly related to the plants in an association, and used in determining the comparative xerophytism of plant habitats in so far as they are determined by atmospheric conditions. In such determinations it would appear that the true measure of the limiting atmospheric factors must be found either in the demand throughout the entire growing season as expressed in the average evaporation rate for that period, or in a maximum demand of several days' duration occurring at a period when the water-supply in the soil is deficient, such as would be expressed in a high rate continuing for a week or more in the latter part of the summer. In the associations studied, these demands show practically the same ratio when compared with one another (figs. 5 and 6). If this be the case, we have in the Livingston or Transeau atmometers instruments of sufficient precision to furnish the most valuable quantitative data in the study of plant associations.

A complete study of the water relations of a habitat may be obtained by combining the data supplied by the atmometer with quantitative determinations of the available soil-moisture. It is hoped that some such data may be available in the near future.

It seems highly desirable, in investigations of this character, that the different investigators employ instruments standardized to the common unit recommended by LIVINGSTON (5), and further that a plant association of wide distribution be used as a basis of comparison, and that the conditions in other associations be expressed in terms of these units whenever it is possible to do so. As no association is more widely spread in the United States than the climax mesophytic forest which is frequently characterized by the presence of either *Acer saccharum* or *Fagus grandifolia*, or

both, so no unit seems so well suited for this purpose as the beech-maple forest association or its ecological equivalent. Thus it may be said that the atmospheric conditions in the lower stratum of the cottonwood dune association during the growing season are 260 per cent as severe for plant life as those in the same stratum of the standard association (the beech-maple forest) during the same period.

The writer hopes to continue and extend these investigations during the coming seasons.

Grateful acknowledgment is made of the helpful advice and suggestions of Dr. HENRY C. COWLES, under whose direction this investigation has been conducted.

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# THE TETRANUCLEATE EMBRYO SAC OF CLINTONIA

R. WILSON SMITH

(WITH PLATE V)

The following results are published in the belief that from the standpoint either of morphology or of phylogeny it is important we should become acquainted with the variations of the angiosperm embryo sac. By searching out and comparing all deviations from the normal type, we may hope to ascertain the directions in which the embryo sac is varying at the present time, and perhaps we may also discover some clue to the path along which it has come. The results here given were obtained from a study of *Clintonia borealis*, collected in the neighborhood of Toronto and of Lake Joseph, Ontario.

The youngest ovaries, collected May 9, showed the ovules already completely anatropous, each with a large archesporial cell, having its nucleus in the synapsis stage (fig. 1). The archesporial cell undergoes no cell division, neither cutting off a parietal cell nor dividing into megaspores, but, as in many liliaceous ovules, passes directely into the embryo sac. Its nucleus, however, suffers a twofold reducing division which is of considerable interest.

The nucleus in the synapsis stage is very large; it is usually situated slightly below the middle of the cell, and occupies fully four-fifths of its width. In the condition represented in fig. 2, the protoplasm is becoming denser about the periphery of the nucleus in preparation for spindle formation, and the loops of chromatic material are beginning to separate and spread throughout the nuclear space. Subsequently, when the fibrils of the spindle are quite distinct, the chromatin is found segmented into chromosomes, which frequently appear in the x's, y's, and other forms, characteristic of the heterotypic division.

The number of these chromosome pairs I have not been able to determine with certainty, since the nucleus is too large to be included in one section. Further, since all my sections are cut

longitudinally to the ovule and therefore at right angles to the equatorial plate, it is difficult to make an accurate count of the chromosomes at a later stage of the mitosis. It is certain, however, that we are here dealing with the haploid number, probably 12. In vegetative divisions 20 or more chromosomes can easily be counted, though in this case also it is not easy to determine the number with certainty. The chromosomes when drawn into the equatorial plate are short and thick, almost globular, strongly contrasting in this respect with the long, crowded chromosomes of the vegetative division.

In none of my material, though careful examination was made, could there be found any difference in the separating chromosomes (fig. 3). Those going to the lower pole are fully as large and give the same staining reaction as those going to the upper pole. But on arriving at the poles of the spindle, the two groups behave very differently. Those at the upper pole unite into a normal nucleus, while those reaching the lower pole fuse together into an irregular lump, without spongioplasm or distinct nuclear membrane. Frequently chromosomes or chromosome fragments fail to reach the principal mass, and remain scattered along the spindle or in the cytoplasm outside. When Flemming's triple stain is used, these fragments, as well as the large chromatic lump, take only the safranin and appear semitransparent, while the chromatin of the upper nucleus, taking the gentian violet, appears dark and opaque. No wall is run in at the close of this division, but a distinct cell plate is formed by the thickening up of the spindle fibers (fig. 4).

Division follows in each of the daughter nuclei resulting from the heterotypic mitosis. My material, however, does not furnish any examples of the prophase of this division, nor any information with respect to the chromosomes. The telophase is represented in figs. 5 and 6. In both figures the remains of the first spindle and its cell plate are still distinguishable (on the left side of fig. 6). A cell plate is formed also on the second spindles, but these and the earlier cell plate are transient structures and disappear shortly.

The division of the upper nucleus results in this case also in the formation of an upper healthy nucleus and a lower irregular lump of chromatin. By the division of the lower of the daughter

nuclei two such lumps are formed. Thus the embryo sac now contains an upper healthy nucleus and three lumps of chromatic material without spongioplasm. The commonest arrangement is that of figs. 6 and 7 rather than fig. 5, the healthy nucleus being somewhat above the middle of the cell and much smaller than the nucleus of the mother cell.

These successive divisions, especially the second, must be completed very rapidly, if one may judge from the rarity of their occurrence in the material. Thus, of about 350 ovules in the stages represented by figs. 2–7, more than 225 were in synapsis, and only 5 in the second division.

It can scarcely be doubted that the four nuclei just described are the four megaspore nuclei, and that megaspore formation in *Clintonia* differs from the normal type simply by omitting the formation of walls and by an earlier beginning of the degeneration of the sterile megaspores.

It is clear that division of the imperfect nucleus formed by the heterotypic mitosis can be of no importance in the subsequent history of the embryo sac; yet among 80 embryo sacs of the age of fig. 7, there was not one in which the lower nucleus had failed to divide. The three sterile nuclei could be found in every case. This fact would imply a strong hereditary tendency to a second division, such as we might expect to accompany megaspore formation; and incidentally it would indicate that the impulse to nuclear division must originate in the cytoplasm, since so imperfect a nucleus cannot be regarded as capable of exercising any of the functions of a normal nucleus.

A second peculiarity of the embryo sac of *Clintonia* is its unipolarity. Only two divisions of the megaspore nucleus occur, and thus are produced four nuclei which, in their position, relation to one another, and later behavior, exhibit the characteristics of the four upper nuclei of a normal embryo sac. The change from megaspore to mature embryo sac, involving two nuclear divisions, requires an interval of about three weeks, and it is therefore difficult to obtain karyokinetic figures. That those I have been able to secure are in the late phases is probably due to slow infiltration of the fixing medium.

The fertile megaspore nucleus moves to a higher position and rests for some time. The spindle of the first division is parallel to the axis of the embryo sac, and the two nuclei formed are always one above the other, as in figs. 8 and 9. Again at this division a temporary cell plate is formed. The second division occurs simultaneously in the two nuclei, and the spindles are at right angles to each other. The two upper sister nuclei and the protoplasm about them become the synergids; of the other two, one surrounded by vacuolated protoplasm and a plasma membrane becomes the egg, and the remaining one is a free nucleus, in position and appearance the upper polar.

Usually at these stages some remains of the sterile nuclei are still recognizable, but it is not always possible to be sure all three are present. They stain much less deeply than when first formed, taking little safranin and appearing to have a dark color of their own, independent of the stain. They vary considerably in size, and very frequently appear pitted or vacuolated, as in fig. 9. They are usually situated in the lower end of the embryo sac, as in figs. 8 and 11; fig. 9 is an exceptional case, since one of the sterile nuclei appears in the micropylar region.

Up to the tetrad stage the protoplasm of the embryo sac shows no tendency to unipolarity; it is coarsely granular and evenly distributed. But after the first division of the megaspore nucleus, when there is considerable enlargement of the sac, the protoplasm of the antipodal region becomes scant and stringy with large irregular vacuoles; that of the micropylar region is much denser, and the numerous vacuoles, which appear only at a late period, are small and globular.

A third peculiarity of *Clintonia* is its comparative sterility. Though it blossoms freely, only a very small proportion of the flowers result in fruit. Propagation by vegetative outgrowths of the rhizome is the common means of multiplication. An examination of 50 ovaries, collected one week after the opening of the flowers, disclosed no embryos and no certain proof that fertilization had occurred. In several embryo sacs one of the synergids was partially disintegrated, and in two cases two free nuclei were found below the egg apparatus, presumably derived from division

of the polar nucleus. Whether or not fertilization occurs normally in those ovaries which develop into fruit, I am at present unable to say, nor can I assign the cause of the large proportion of abortive flowers. Apparently it is not due to any imperfection in the microspore, which contains two normal nuclei and appears plump and healthy.

An attempt to estimate the percentage of fertile flowers by field observation proved futile. An area producing 550 flowers was kept under observation and undisturbed, but all to no purpose. The flowers one and all were abortive, and two weeks after opening had withered and fallen away, leaving only the shriveled pedicels.

An attempt also was made to determine whether the sterility is due to imperfect pollination. A small number of flowers were artificially pollinated, but these like the others yielded no seeds. However, as several days of heavy rain interfered with the experiment, I cannot regard it as conclusive.

## Discussion

The interpretation of the embryo sac of *Clintonia* is made easier by recent investigations of certain Onagraceae. GEERTS (**6**) finds that in *Oenothera Lamarckiana* the single archesporial cell gives rise to a tetrad row of megaspores, of which the uppermost develops, slowly absorbing the three lowermost and producing four nuclei arranged much as in *Clintonia*. The same condition is reported by MODILEWSKI (**10**) as occurring in *Epilobium angustifolium*, *E. Dodonaei*, *Oenothera biennis*, and *Circaea lutetiana;* in all these the unipolarity of the embryo sac is strongly marked and there is "double fertilization." A comparison of the embryo sac development of these and of *Clintonia* makes it clear that the four nuclei of figs. 5–7 represent four megaspores. Further, in these six species the unusual condition prevails of having the upper megaspore fertile. The chief differences shown in the development of *Clintonia* are in the absence of walls separating the megaspores and in the large proportion of sterile ovules.

A nearly similar embryo sac occurs in *Oenone* and *Mourera*, two genera of the Podostemaceae examined by WENT (**14**). A mother cell after synapsis divides into two; the upper of these

after division of its nucleus gradually disintegrates; the lower cell also gives rise to two nuclei, one of which, the lower, becomes a mere clump of chromatin, while the other divides twice and the four resulting nuclei arrange themselves as in *Clintonia* and the above named Onagraceae. Though WENT does not discuss the theoretical value of the first four nuclei derived from the mother cell, it seems clear they represent megaspores, of which that next the innermost is the fertile one. Thus two megaspores appear in the upper cell, and two in the lower cell which becomes the embryo sac. The development of one of the middle megaspores, although uncommon, is not unknown. It has been seen in *Acacia* and *Eriobotrya* (GUIGNARD 1881, 1882), *Trapella* (OLIVER 1888), some of the Araliaceae (DUCAMP 1902), and *Asclepias* (FRYE 1902); to this list, which is taken from COULTER and CHAMBERLAIN'S *Angiosperms*, may be added *Vaillantia* and *Collipeltis* (LLOYD 1902).

In the examples thus far reviewed, the four functional nuclei of the embryo sac are the direct derivatives of one of four megaspores. Some cases of a different nature remain for consideration. In *Limnocharis* (HALL 1902) tetrads are not formed; the first two nuclei of the mother cell place themselves at opposite poles, and while the upper gives rise to the egg apparatus and a polar nucleus, the lower remains undivided. Nearly similar is *Helosis*, but in this case the primary antipodal nucleus soon degenerates (CHODAT and BERNARD 1900; I have not been able to consult the original paper). *Cypripedium* (PACE **11**) furnishes another example of a tetranucleate embryo sac. In this plant the mother cell divides once and the lower of the two daughter cells becomes the embryo sac, its nucleus undergoing two divisions. Miss PACE interprets the first two nuclei of the embryo sac as megaspore nuclei. Thus according to this view the embryo sac of *Cypripedium* is compound, being the product of two megaspore nuclei.

Miss PACE extended the conception of a compound embryo sac to *Lilium*, in which four megaspores are thought to function, and more recently COULTER (**4**) has extended it to all those cases in which tetrad formation is apparently suppressed, and especially to the 16-nucleate embryo sac of *Peperomia* and the like.

McALLISTER's (**7**) discovery of temporary walls separating the first four nuclei of the embryo sac of *Smilacina*, which otherwise resembles *Lilium*, is strongly confirmatory of this interpretation. Though the results of the present paper have no direct bearing upon this question, it may be pointed out that in *Clintonia* and the Onagraceae we see for the first time a mature gametophyte of four nuclei proceeding from an indubitable megaspore; and the occurrence in the Penaeaceae (STEPHENS **12**) and *Euphorbia procera* (MODILEWSKI **9**) of four symmetrically placed groups of nuclei, each group similar in appearance to the gametophyte of *Clintonia*, certainly suggests a similar origin for each group. No case is yet known of a 16-nucleate embryo sac derived from one of four megaspores. In *Peperomia* (BROWN **1**) and the Penaeaceae (**12**) there are no tetrads, and reduction occurs in the embryo sac. In *Euphorbia procera* the history has not been traced back to the mother cell. In Gunnera[1] also (MODILEWSKI **8,** ERNST **5**) there are no tetrads. The case of *Pandanus* (CAMPBELL **3**) offers some difficulty; the embryo sac is said to be one of three sporogenous cells (presumably megaspores). But CAMPBELL did not obtain evidence where the reduction divisions occur, and the view that in the group of three "sporogenous cells" the upper two are parietal cells rather than megaspores is a fair inference from his figures and data. The point certainly needs further investigation.

*Clintonia*, *Eichhornia* (SMITH 1898), *Avena* (CANNON 1900), and *Asperula* (LLOYD 1902) give us examples of four megaspores in one sac, and in *Crucianella* LLOYD (1902) found all four megaspores germinating within the one wall. No one doubts that these are megaspores, simply because three of them or their products disintegrate. But surely the weightier evidence is that of chromosome reduction, and this applies equally to *Lilium*, *Peperomia*, etc. This is the position taken by COULTER (**4**). He maintains that in the genesis of the angiosperm embryo sac "the essential part of the process is found in the first two divisions," and he adds "megaspores, at least their nuclei, cannot be omitted." BROWN (**2**) thinks we cannot make chromosome reduction the sole test of

[1] ERNST understands SCHNEGG (1902) to assert the occurrence of tetrads in *Gunnera Hamiltoni*, but the latter author does not figure tetrads nor use the word, and it seems probable his "Viertheilung" refers to nuclear and not to cell division.

megaspore formation, and he proposes a different criterion. "A distinction," he says, "between the first division of a megaspore and a division giving rise to megaspores is that while in the first case no cell plate is formed on the spindle, in the latter case either a wall or a cell plate is formed on the spindle." BROWN admits the compound nature of the embryo sac of *Lilium* and *Peperomia*, but for the reason just quoted refuses to admit it in the case of *Cypripedium*. To be consistent, he ought not to allow it for *Lilium*, since in this case a cell plate is formed in the third mitosis of the embryo sac. His distinction breaks down, however, in the case of *Clintonia;* in fig. 8 the first division of the megaspore nucleus is accompanied by a cell plate. It seems to the writer that the general principle of a compound embryo sac, while not altogether free from difficulties, furnishes the explanation of a large number of abnormal embryo sacs.

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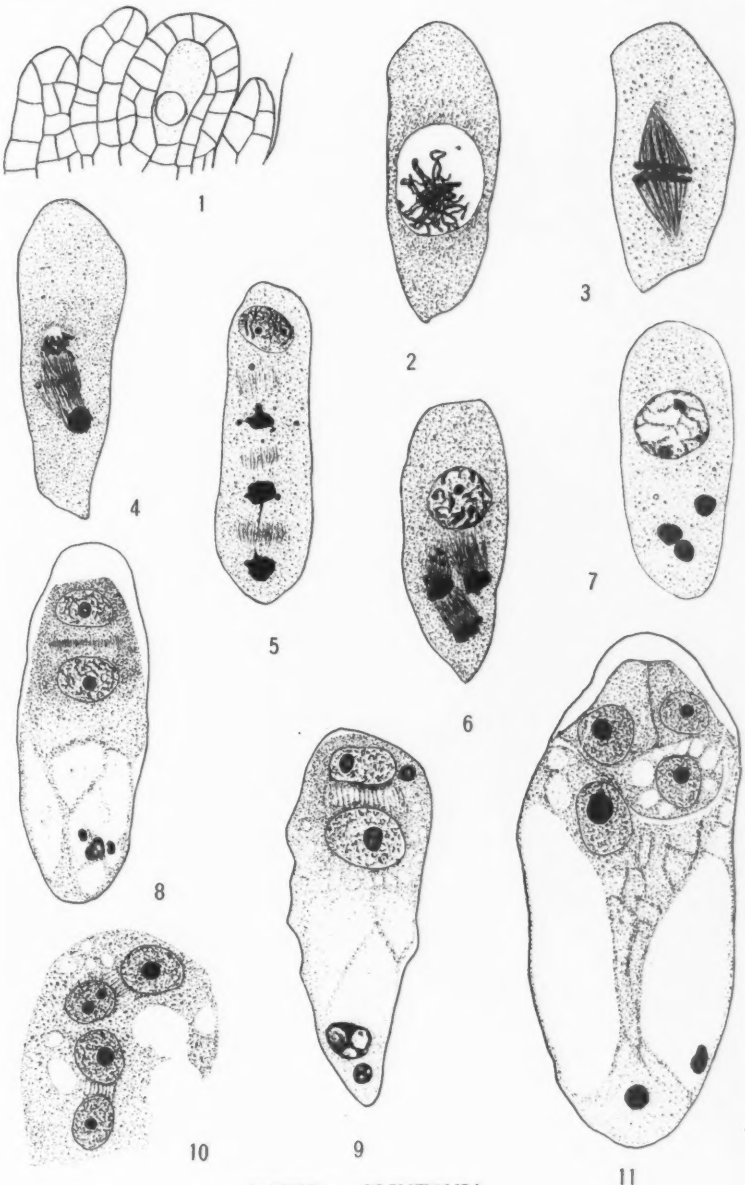


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## EXPLANATION OF PLATE V

All the figures were drawn with the aid of an Abbé camera lucida on a Leitz microscope. For fig. 1, ocular 1 and objective 7 were used; for all the others, a 2 mm., 1.30 aper. apochromatic immersion lens with compensation ocular 4. The drawings have been reduced one-half in reproduction.

FIG. 1.—Apex of nucellus with megaspore mother cell.

FIG. 2.—Megaspore mother cell with nucleus emerging from synapsis.

FIGS. 3, 4.—First mitosis in megaspore mother cell.

FIGS. 5, 6.—Second mitosis in megaspore mother cell.

FIG. 7.—Megaspore mother cell with four megaspore nuclei, one healthy and three degenerate.

FIGS. 8, 9.—Embryo sac showing first division of fertile megaspore nucleus.

FIG. 10.—The apex of an older embryo sac.

FIG. 11.—Embryo sac of a fully opened flower; in this, as in all the others, there are no antipodals.

# THE EMBRYO SAC OF PHYSOSTEGIA[1]

LESTER W. SHARP

(WITH PLATES VI AND VII)

The material of *Physostegia virginiana* (L.) Benth., upon which the present work is based, was collected near Alma, Michigan, in August 1909. Although the investigation has brought out no new point of fundamental importance, the results are deemed worthy of record.

The ovule arises from the floor of the sporangial chamber as a small protuberance, which in growing pushes out the ovary wall in such a manner that it becomes completely surrounded by the latter except at the funiculus. At the time when the archesporium is distinguishable as a single hypodermal cell, the young ovule is slightly curved, and as growth proceeds this curving becomes more pronounced, until finally an anatropous condition is reached. A single massive integument is developed.

The archesporial cell, which cuts off no parietals, grows rapidly, and is markedly elongated at the time when its nucleus goes into synapsis preceding the first division (fig. 1). This cell, which, on account of the occurrence of the heterotypic prophases in its nucleus, is to be regarded as the megaspore mother cell, by two successive divisions gives rise to a row of four megaspores (fig. 2). Of these the outer three degenerate (fig. 3), while the innermost enlarges and gives rise to the embryo sac.

The nucleus of the functioning megaspore divides, and the two daughter nuclei take up positions near opposite ends of the sac, which becomes strongly curved, and, owing to rapid growth, develops a large central vacuole (fig. 4). Each nucleus divides, forming the four-nucleate stage (fig. 5). These four nuclei by one further division give rise to eight, and walls soon form, resulting in their organization into a typical egg apparatus, three antipodal

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 20.

cells which soon multiply to several, and two free polar nuclei (fig. 6).

Shortly before the division to form eight nuclei, a laterally directed lobe begins to develop from the antipodal region of the sac, and at the eight-nucleate stage is very conspicuous (fig. 6). It rapidly invades the integumentary tissue, forming what may for convenience be called the "endosperm lobe," since it is soon to contain nearly all of the endosperm formed. During these early stages it probably serves in a haustorial capacity, as does the greatly enlarged antipodal portion of the embryo sac of *Saururus* (JOHNSON 7).

Meanwhile the micropylar polar nucleus migrates to the narrow portion of the sac near the antipodals, where it meets and fuses with the polar nucleus of the antipodal group. The resulting fusion nucleus is invariably found in this position (fig. 7).

At about this time the antipodal cell which lies nearest the sac cavity takes on an appearance different from that of the others. It becomes binucleate, the cytoplasm changes in character, staining more deeply, and rapid enlargement causes its wall to become strongly convex (fig. 7). This enlargement continues until the cell bulges out conspicuously into the embryo sac cavity (fig. 10), and its wall thus partitions off the small pocket in which it lies with the other antipodals. In stages somewhat later it bears much resemblance to the first few cells of the endosperm, but the possibility that it also is of endospermous origin is precluded by the fact that it has been observed side by side with an undoubted endosperm nucleus resulting from the triple fusion (fig. 9).

The function of the cell in question is in all probability haustorial, recalling the behavior of the basal antipodal in several genera of the Galieae (LLOYD 10), although in the sac under consideration the neighboring tissue is not actively invaded. It soon fills all the space formerly occupied by the other antipodals, which disorganize and completely disappear (figs. 13, 14, 16), while in its general form and relation to the vascular supply it is especially well suited to the performance of a nutritive function during the rapid development of the endosperm. Later it disappears and the tissue of the region becomes irregularly broken down (figs. 18–20).

The great variety in form and behavior exhibited by antipodal cells, together with haustorial structures of many types, has been so well summarized (COULTER and CHAMBERLAIN 3) that further comment here is unnecessary, since *Physostegia* offers nothing essentially new.

At the time of fertilization the general aspect of the embryo sac, together with its position in the ovule and its relation to the vascular supply, are as shown in fig. 8. The usual configuration of the egg apparatus is that figured here, but in other cases it exhibits considerable variation from this. In regard to the positions of the nuclei and vacuoles, the synergids represented in fig. 7 show striking similarity to the egg, and it is conceivable that at least the larger one might function as such.

The pollen tube, which has grown down the style into the sporangial chamber, makes its way around the stalk of the ovule, or at times directly over its summit, to the micropyle, through which it enters the embryo sac. Clear cases of fusion of the male nucleus with that of the egg were not observed, but the presence of the pollen tube within the sac, the disorganization of the synergids, the immediate elongation of the egg with divisions to form an embryo, and a triple fusion in the central region of the sac (fig. 9) make it reasonably safe to conclude that fertilization of the usual type occurs.

The formation of the endosperm is of considerable interest. It is initiated by the division of the endosperm nucleus, which occurs in the narrow region of the sac near the haustorial antipodal, as shown in fig. 10. The spindle has a transverse orientation and is very broad, owing to the large number of chromosomes present. The division is accompanied by a longitudinal wall running through the middle of the sac, as shown in fig. 11, which represents a sac cut in a plane at right angles to that of fig. 10. Here the wall is still in process of formation, spindle fibers being evident at its extremities. Extension continues until it comes into contact with the sac wall at or near the end of the endosperm lobe (fig. 12), while in the micropylar lobe it was not observed to do so, and probably ends freely. The nuclei now lying in the two resulting parts of the embryo sac divide, forming transverse

walls (fig. 12), and further similar divisions give rise to a large-celled, thin-walled tissue which fills the endosperm lobe (fig. 13). This endosperm formation may cease abruptly at the narrow portion of the sac (fig. 14), but usually extends for a little distance into the micropylar lobe (fig. 16). The two-ranked arrangement so conspicuous in the endosperm lobe in fig. 13 and in the micropylar lobe in fig. 16 is doubtless due to the longitudinal separation of the embryo sac into two parts as described above.

The cessation of endosperm formation at an indefinite point results in nuclei being left free in the cytoplasm of the micropylar portion of the sac (fig. 13). These nuclei, usually two in number, enlarge (fig. 14) and may occasionally divide, the walls which appear on the spindle fibers being evanescent. Often the nuclei were observed fusing. Consequently, from one to at least four may be present in stages somewhat later, but they play no further active part, and disorganize with the other contents of the micropylar lobe (figs. 18 and 19).

In embryo sacs which show a wall at the first division of the endosperm nucleus it is usual for the sac to be thereby separated transversely into two chambers, and for endosperm to be formed only in the micropylar one. Among such cases the endosperm may pass through a free nuclear stage, as in *Sagittaria* (SCHAFFNER 12), *Limnocharis* (HALL 5), and *Ruppia* (MURBECK 11); or walls may be formed at all of the divisions, as in *Ceratophyllum* (STRASBURGER 13) and the *Nymphaeaceae* (COOK 1 and 2). Less frequently both daughter nuclei resulting from the division of the endosperm nucleus take equal parts in the direct formation of cellular endosperm, as reported for *Peperomia pellucida* (JOHNSON 8), *Heckeria* (JOHNSON 9), and *Datura laevis* (GUIGNARD 4). From the above account it is seen that essentially this is the mode of endosperm formation in *Physostegia*, and in this sac the main point of interest lies in the fact that the first wall is longitudinal rather than transverse. The factors governing the orientation of the spindle and the consequent position of the wall are not at all clear, and the feature is probably best regarded as a minor peculiarity rather than a character of much significance.

The restriction of endosperm to the antipodal portion of the

embryo sac has been observed in a number of cases (COULTER and CHAMBERLAIN **3**), the condition reaching its extreme in *Loranthus* (HOFMEISTER **6** and TREUB **14**), in which scarcely more than the lower one-tenth of the sac becomes filled with permanent endosperm tissue. Among the Labiatae the work of TULASNE (**15**), HOFMEISTER (**6**), and VESQUE (**16**) shows this to be the prevailing condition in several genera. In *Stachys sylvatica* TULASNE figures endosperm developing in the antipodal region of a slightly curved sac, but without the presence of a special chamber; and in *Betonica* a condition which may well represent a later stage in the same situation. The figures of HOFMEISTER indicate that in *Lamium* the endosperm lobe is well developed before fertilization, as in *Physostegia*. Although no antipodals and only two "Keimbläschen" are represented, HOFMEISTER has figured stages which correspond approximately to those shown in figs. 7, 8, 14, and 16 of this paper.

In all of these cases the embryo is brought into contact with the endosperm by the great elongation of the micropylar cell of the proembryo. The earliest clearly observed stage in *Physostegia* is shown in fig. 13. Here the first division in the fertilized egg has occurred, and the micropylar cell by its great elongation is pushing the chalazal cell into the endosperm, the cells of which at this time are relatively few in number. Nearly all the elongation is accomplished by the one cell, but this soon divides to several (figs. 14 and 16).

The first division in the chalazal cell is longitudinal (fig. 15), as is also the second. Each of the four resulting cells is then divided into two by a transverse wall (fig. 16), and the subsequent divisions proceed with much regularity (figs. 17 and 18).

At the time when the embryo becomes imbedded in the endosperm, the micropylar and endosperm lobes are approximately equal in size. The former, as has been noted above, disorganizes and in later stages becomes entirely obliterated, while the latter increases rapidly in size owing to the active growth of the endosperm. This growth is accomplished at the expense of the cells of the integument, which in the mature seed is recognizable as only one or two layers of cells (figs. 19 and 20). At the same time the

embryo grows rapidly, becomes characteristically dicotyledonous, and displaces nearly all of the endosperm. It attains a length of nearly 2 mm. in the mature seed, the coat of which is formed from the ovary wall.

## Summary

1. The archesporium of *Physostegia* consists of a single hypodermal cell, which, without formation of parietals, functions as the megaspore mother cell.

2. The megaspore mother cell by two successive divisions gives rise to a row of four megaspores; the chalazal one enlarges and gives rise to the embryo sac, while the other three disorganize.

3. The mature embryo sac contains an egg, two synergids, three antipodal cells which multiply to several, and two polar nuclei which fuse.

4. During the formation of the embryo sac a lobe develops from near its chalazal end, so that the sac consists of two distinct parts joined by a narrower portion.

5. Double fertilization of the usual type in all probability occurs.

6. The endosperm is cellular from the beginning, the wall accompanying the first division of the endosperm nucleus being longitudinal through the sac. The chalazal portion of the sac, or "endosperm lobe," becomes completely filled with endosperm tissue, which invades and destroys nearly all of the integument; while the micropylar portion of the sac never contains more than a very few endosperm cells, and later disorganizes, becoming completely obliterated by the encroaching endosperm.

7. The first division in the fertilized egg is transverse, and the chalazal cell, which becomes imbedded in the endosperm through the great elongation of the micropylar cell, develops very regularly into a typically dicotyledonous embryo, which displaces nearly all of the endosperm.

This investigation was carried on under the direction of Professor D. S. JOHNSON, to whom the writer is indebted for many helpful criticisms.

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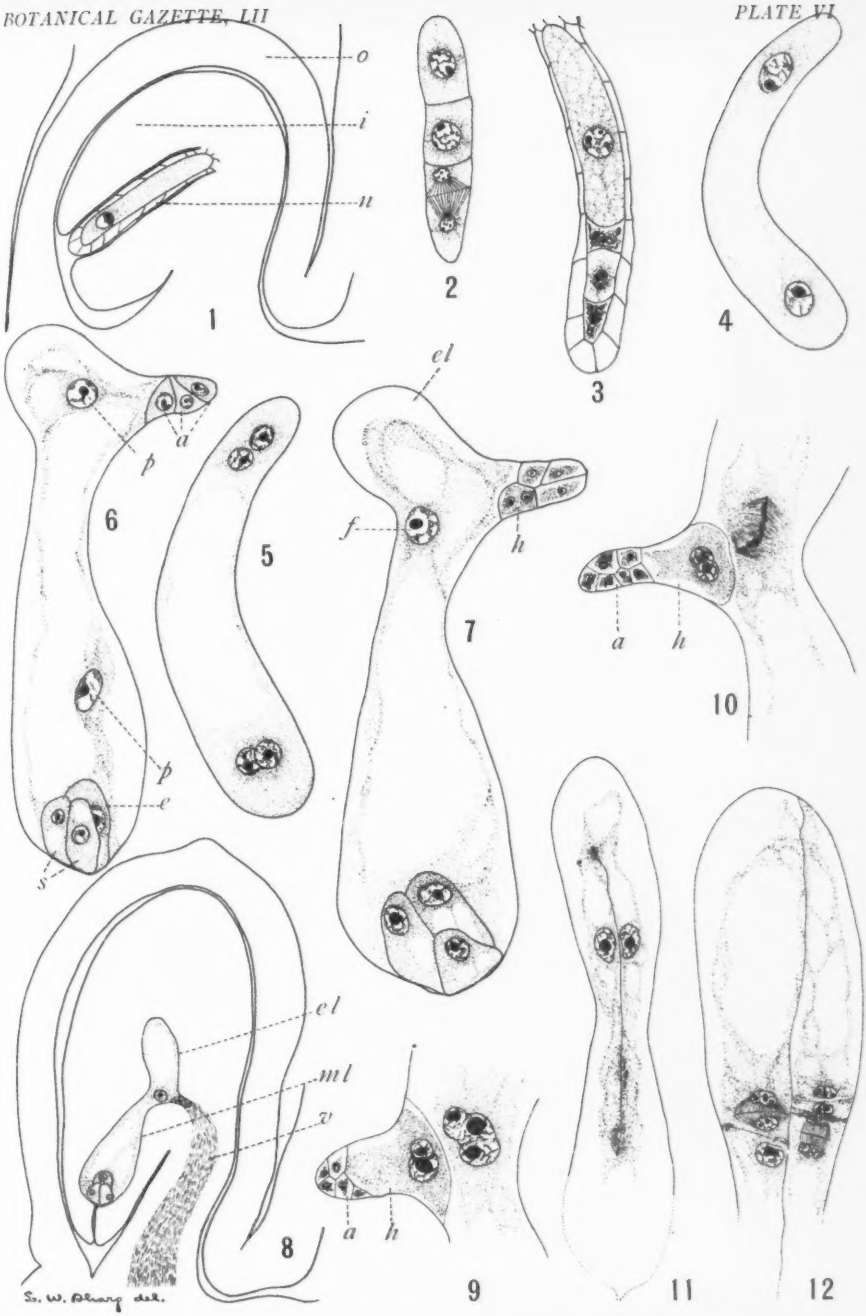
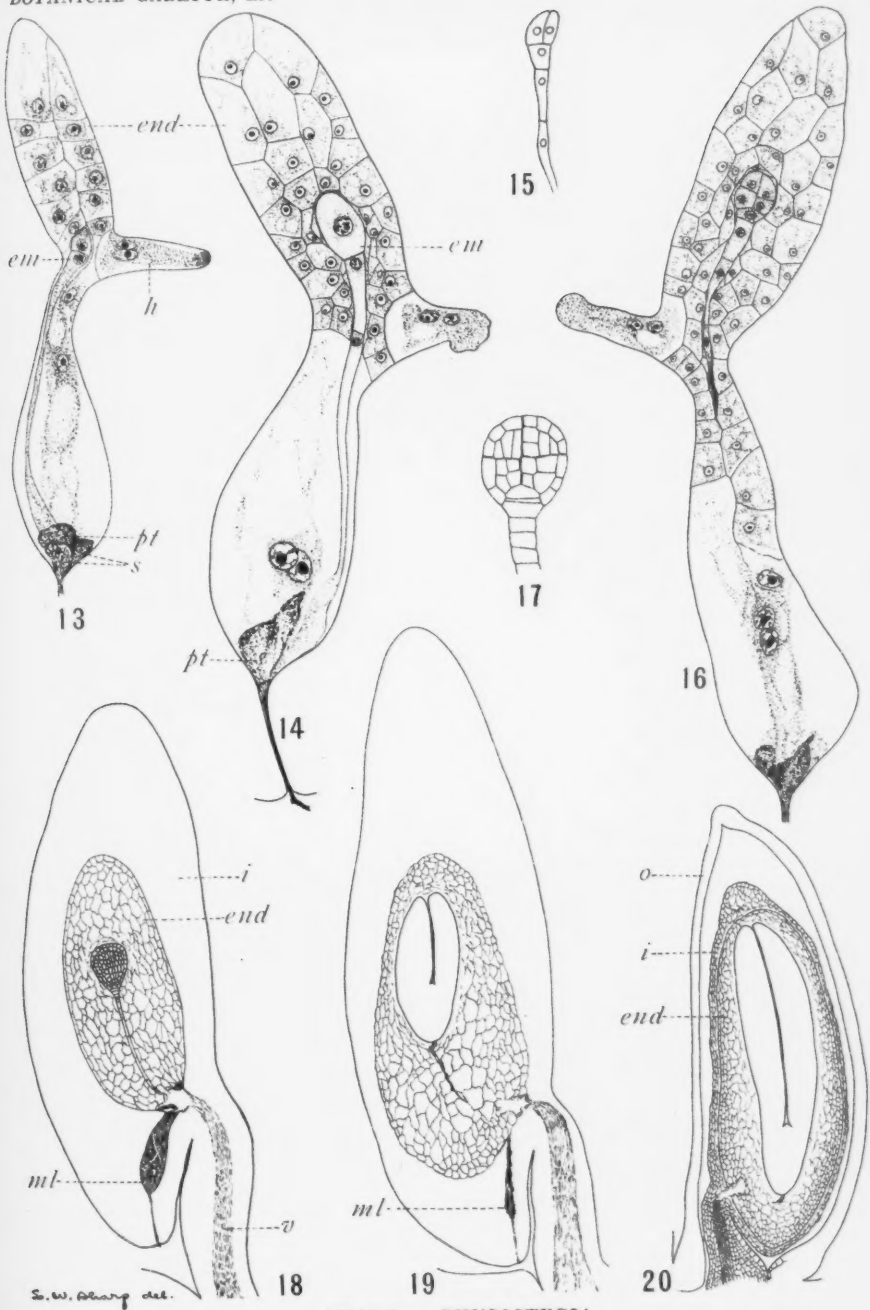



SHARP on PHYSOSTEGIA




SHARP on PHYSOSTEGIA

## EXPLANATION OF PLATES VI AND VII

All figures were drawn with the aid of an Abbé camera lucida, have a corresponding orientation, and show magnifications as follows: figs. 1, 11, 13–17, ×215; figs. 2–5, 9, ×462; figs. 6, 7, 10, 12, ×385; fig. 8, ×81; figs. 18, 19, ×45; fig. 20, ×25. The following abbreviations are used: *a*, antipodals; *e*, egg; *el*, endosperm lobe; *em*, embryo; *end*, endosperm; *f*, fusion nucleus; *h*, haustorial antipodal; *i*, integument; *ml*, micropylar lobe; *n*, nucellus; *o*, ovary wall; *p*, polar nucleus; *pt*, pollen tube; *s*, synergids; *v*, vascular supply.

*PLATE VI*

FIG. 1.—Young ovule with archesporial cell nucleus in synapsis.

FIG. 2.—Four megaspores; the division to form the two micropylar ones is delayed.

Fig. 3.—Four megaspores; the innermost one much enlarged, the other three disorganizing.

Fig. 4.—Two-nucleate embryo sac.

FIG. 5.—Four-nucleate embryo sac.

FIG. 6.—Eight-nucleate embryo sac.

FIG. 7.—Mature embryo sac; the polar nuclei have fused and the antipodals have increased in number; one antipodal beginning to differentiate as a haustorial cell.

FIG. 8.—Ovule with mature embryo sac.

FIG. 9.—Triple fusion of male and polar nuclei; haustorial antipodal cell present; other antipodals disorganizing.

FIG. 10—First division of endosperm nucleus.

FIG. 11.—Daughter nuclei resulting from first division of endosperm nucleus; the wall accompanying the division is still in process of formation.

FIG. 12.—Subsequent endosperm divisions, all accompanied by walls.

*PLATE VII*

FIG. 13.—Two-celled proembryo coming into contact with the endosperm; haustorial antipodal cell well developed; the other antipodals and the synergids have degenerated.

FIG. 14.—Later stage; endosperm formation has ceased abruptly at the narrow portion of the sac in this case.

FIG. 15.—Chalazal cell of proembryo divided longitudinally.

FIG. 16.—Somewhat later stage; the endosperm has extended into the micropylar lobe.

FIG. 17.—Later stage of embryo.

FIG. 18.—Endosperm invading integument; embryo digesting endosperm; haustorial antipodal cell and micropylar lobe disorganized.

FIG. 19.—Later stage.

FIG. 20.—Section of nearly mature seed; the embryo has used up the greater part of the endosperm, which in turn has obliterated nearly all of the integument; seed coat formed from the ovary wall (*o*).

# THE BRAZIL NUT[1]

W. J. YOUNG

(WITH PLATE VIII AND ONE FIGURE)

The genus *Bertholletia*, to which is assigned the Brazil nut of commerce, was established in 1808 by HUMBOLDT and BONPLAND, who placed in it a single species, *B. excelsa*. A translation of BONPLAND'S description of the fruit of this species is as follows:[2]

> Fruit a spherical, compound nut the size of a child's head and often larger, divided internally into four cells, each of which encloses several nuts; covered on its exterior with a husk of a green color, smooth and shining.
>
> Main nut very solid, rough and marked by branching furrows on its outer surface, 6 lines (1 cm.) thick, divided internally into four cells by as many membranous dissepiments which become obliterated in part or entirely after the maturity of the fruit, but of which there always remain traces.

The tree is described as 33 m. high, with a trunk 9 dm. in diameter. Leaves alternate, oblong, subcoriaceous, 1 dm. broad and 6 dm. long, borne on short petioles. Type locality, Rio Orinoco.

On account of the great height of the trees, these botanists were unable to obtain the flowers, although it is said that they offered in vain an ounce of gold for specimens.[3] On this account, they were uncertain as to the position which the genus *Bertholletia* should occupy. More recent investigations have established it next to *Lecythis* among Lecythidaceae, an arrangement now universally accepted. It is worthy of note, also, that BONPLAND failed to describe either the operculum or the opercular opening of the fruit, although the latter is shown in his drawing as becoming decidedly narrower at the inner edge.

For more than half a century after the publication of BONPLAND'S description of *B. excelsa*, the genus was accepted as monotypic. Evidence was being gradually accumulated, however, which led to the recognition of a second species. Among the

[1] Published by permission of the Secretary of Agriculture.

[2] BONPLAND in HUMBOLDT and BONPLAND, Plantes equinoxiales 1:110, 111.

[3] SPRUCE, RICHARD, Notes of a botanist on the Amazon and Andes. Edited by A. R. WALLACE. 1:356. 1908.

later botanists to contribute to this end may be mentioned BERG, who in monographing the Brazilian Lecythidaceae described under *B. excelsa* a species distinct from that of HUMBOLDT and BONPLAND.[4] Although BERG's description is marred by several errors, it is sufficiently accurate to demonstrate that the species described is not the *B. excelsa* of BONPLAND. BERG's drawing of the fruit or pyxidium is moreover quite different from that of BONPLAND.

It remained, however, for Mr. J. MIERS to point out clearly the distinction between the two plants and to describe BERG's species under the name *B. nobilis*.[5]

The more noticeable points of distinction between *B. excelsa* and *B. nobilis* are collected from MIERS's description in the following summary:

| *B. excelsa* Humb. and Bonp. | *B. nobilis* Miers. |
|---|---|
| Tree 100 ft. or more high, with trunk 2.5–3 ft. in diameter. | Tree somewhat taller than *B. excelsa*, with trunk 14 ft. in diameter. |
| Leaves green; petioles 9–18 lines long. | Leaves rufescent; petioles 3–6 lines long. |
| Floral panicle 8 in. long, with single branch nearly equal in length, and nodes $\frac{1}{8}$ in. apart. | Floral panicle 10 in. long, with about 5 short branches, and nodes 0.25–0.5 in. apart. |
| Fruit slightly elongated, 0.16 in. in length. | Fruit approximately spherical, usually under 5 in. in diameter. |
| Cortex of fruit smooth, palish, entire, persistent. | Cortex of fruit comparatively thick and rough, darker, cracking as the fruit dries and tending to loosen and drop off as the fruit is handled. |
| Opercular opening with straight or concave walls, narrowing slightly at its inner edge. | Opercular opening with sharp edge and concave walls, and widening considerably inward. |
| Operculum cylindrical, with roundish, indented apex. | Operculum oval or radially compressed, conical and pointed at the apex. |
| Operculum breaks away and falls from the fruit as the columella shrivels. | Operculum remains attached to remnant of columella and, as the latter shrivels, falls into the cavity of the fruit. |

[4] BERG in MARTIUS' Flora Braziliensis, I. **14**:478.

[5] MIERS, J., On the Lecythidaceae, *Bertholletia*. Trans. Linn. Soc. II. **30**:195–199.

The differences noted above, as far as they relate to the fruit, are well shown in the copy of MIERS's drawing, reproduced half-size in text fig. 1.

The idea that *B. excelsa* Humb. and Bonp. is the source of commercial Brazil nuts has become so thoroughly grounded in popular and even in botanical literature that it seems to be accepted on faith and passes unchallenged. The extent of this belief will be apparent when we consider that of the following quotations only the last two, or possibly three, make any mention of a second species, to which, moreover, they assign a wholly subordinate position.

*Brazil nut.*—One of the triangular edible seeds of a tall South American tre (*Bertholletia excelsa*).—Standard Twentieth Century Dictionary.

*Brazil nut.*—The seed of the fruit of *Bertholletia excelsa.*—Century Dictionary.

*Brazil nut.*—An oily 3-angled nut, the seed of the lecythidaceous Brazilian tree *Bertholletia excelsa.*—Webster's New International Dictionary.

*Cream nut* (*Bertholletia excelsa* Humb. and Bonp.).—This is a common nut in our markets brought from Brazil; hence it is often called Brazil nut.—Nut culture in the U.S., p. 106, Div. of Pomology, U.S. Dept. Agriculture

*Brazil nuts, cream nuts, Para nuts.*—These are edible nuts imported from Brazil. The nuts are the product of *Bertholletia excelsa* (Humboldt and Bonpland).—U.S. Disp., 19th ed., p. 1420.

*Bertholletia excelsa.*—Brazil nut.—A large tree belonging to the family Lecythidaceae, and yielding the Brazil or Para nuts of commerce. A tree 100 to 150 ft. high, distributed throughout northeastern South America to the Island of Trinidad.—COOK and COLLINS, Economic plants of Porto Rico, Contrib. U.S. Nat. Herb. **8**:91. 1903.

*Bertholletia* Humb. and Bonp.—Tall trees. One or two species. South America.

*a. B. excelsa* Humb. and Bonp.—*Seeds*, Brazil nuts, Para nuts, cream nuts, nigger toes, Castana nuts.—LYONS, A. B., Pl. names, sci. and pop., 2d ed., p. 71.

*Bertholletia.*—Brazil nut, Para nut, cream nut, nigger toe.—Species 2, both of which furnish Brazil nuts.—HASTINGS, G. T., in BAILEY'S Cycl. of Hort.

The Brazil nut, also called Para nut, from the port of shipment, is the seed of a large tree (*Bertholletia excelsa* Humb. and Bpl.).—Another species, *B. nobilis* Miers, also yields a similar nut.—WINTON, A. L., Microscopy of vegetable foods, p. 312.

This state of affairs seems to be due primarily to BONPLAND'S assumption, stated in connection with his description of *B. excelsa*,

that it is this species which furnishes the Brazil nut. The long time which elapsed previous to the identification of a second species allowed this view to become so thoroughly established that MIERS's work appears to have been overlooked by persons inter-

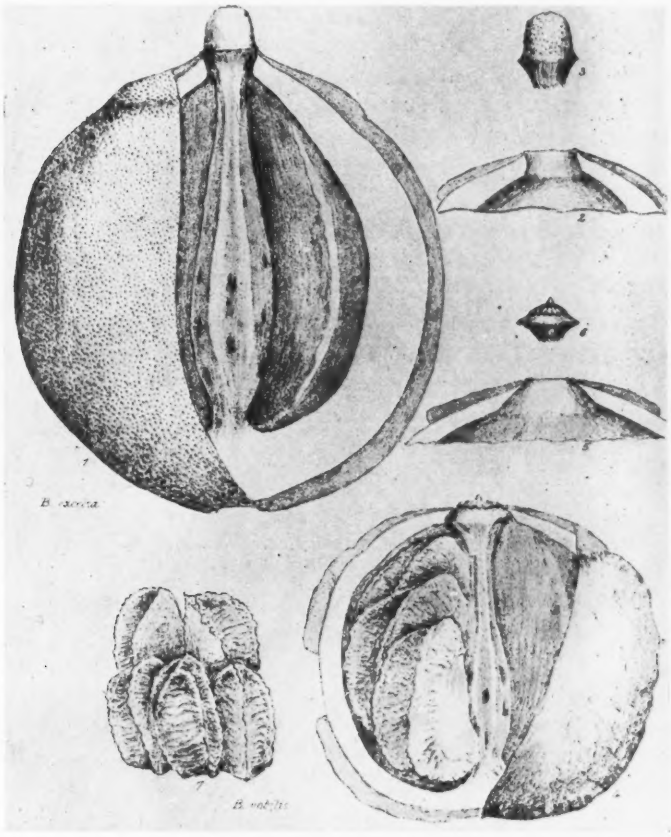


FIG. 1.—Reproduction of MIERS's drawings of *Bertholletia*, copied half-size from Trans. Linn. Soc. **30**: *pl. 37. figs. 1–3, Bertholletia excelsa: 1*, pyxidium cut open to show structure; *2*, section of opercular opening; *3*, operculum; *4–7, Bertholletia nobilis: 4*, pyxidium cut open to show structure; *5*, section of opercular opening; *6*, operculum; *7*, a cluster of seeds (Brazil nuts).—Published by courtesy of the Linnean Society of London.

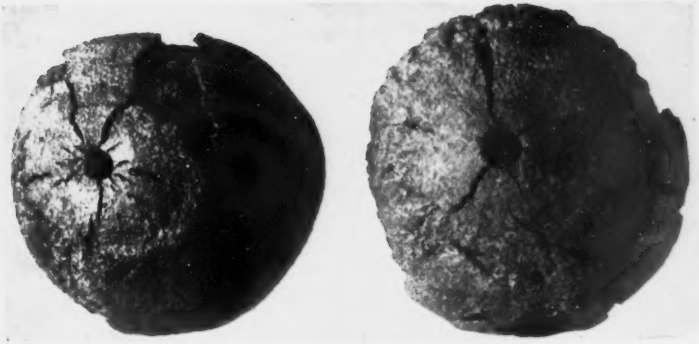
ested in botany from the economic standpoint. The work of various botanists during this interval, and especially BERG'S description of *B. nobilis* under the name *B. excelsa*, no doubt contributed to the same end. Moreover, the seeds of the two species, so far as can be judged from the descriptions and drawings available, are so similar as to be distinguished with difficulty if at all.

After making a careful study of the situation, the writer has become convinced that the commonly accepted view is erroneous, and that the Brazil nuts of commerce are derived from *B. nobilis* Miers (*B. excelsa* Berg) and not from *B. excelsa* Humb. and Bonp. The reasons for this view are given below.

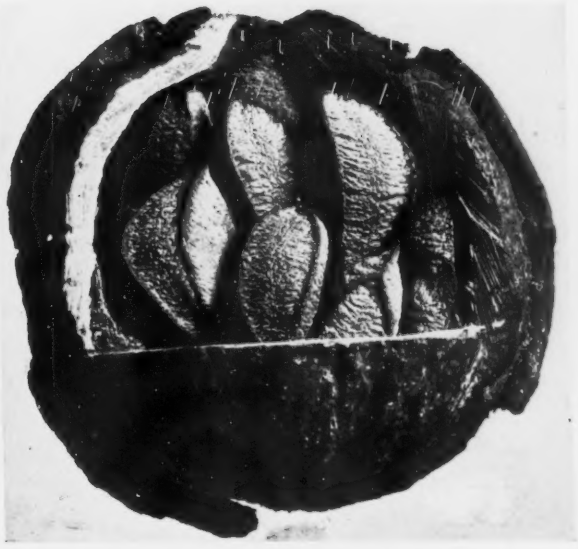
1. Commercial samples of Brazil nuts contain, in larger or smaller numbers, opercula derived from the fruit, and the presence of these in itself is evidence that the nuts were derived from *B. nobilis*, since, as has been noted in the comparison, the opercula fall from the mature pyxidia of *B. excelsa*, and hence would not find their way into samples of nuts from that source. On the other hand, their presence among nuts from *B. nobilis* is perfectly normal and what would be expected, since in this species the opercula fall into the interior of the pyxidia and become mixed with the nuts. Moreover, the opercula, so far as the writer has been able to observe, are always of the *B. nobilis* type, as shown in fig. 1. They vary in form from ovoidal bodies to cones of varying slope, being modified apparently by the size and degree of persistence of the columella, as well as by the extent of the grinding against surrounding nuts to which they have been subjected during shipment. All, however, are provided with a distinct apical point except where it has been broken off, in which case the fact is usually quite evident. It cannot be denied that the absence of opercula of the *B. excelsa* type does not preclude the possibility that nuts of this species may be occasionally mixed with those of *B. nobilis*, since the writer is not aware that it is possible to distinguish the species from the character of the nuts alone.

2. Every pyxidium of the Brazil nut which the writer has had an opportunity to examine has indicated that the fruit is that of *B. nobilis*. Their main points of structure are well shown in

1



2



3

YOUNG on BRAZIL NUT

figs. 2 and 3, which illustrate pyxidia obtained from different sources. A comparison of the photograph with MIERS's description of *B. nobilis* will leave no doubt of their identity. Most if not all of the pyxidia which the writer has examined were brought to this country by the importers of Brazil nuts, and represent the source of the nuts in which they deal.

3. The testimony of others, although comparatively scanty, should not be overlooked, since it is improbable that the authorities quoted as stating that the Brazil nut is the seed of *B. excelsa* have given the matter any exhaustive study. After this description of *B. nobilis*, MIERS states "these seeds are known in commerce as Brazil nuts," and proceeds to give statistics regarding their exportation and use. Moreover, BERG's error regarding *B. excelsa*, although perhaps adding to the confusion, is in reality indirect evidence of the same fact, since it is doubtful whether he would have confused the two species had he not been sure that the specimens from which he made his description were those of the Brazil nut, which he, in common with others of his time, regarded as *B. excelsa*.

NOTE.—Acknowledgment is due Mr. H. C. SKEELS of the Office of Foreign Seed and Plant Introduction, U.S. Dept. of Agriculture, who has reviewed the work and confirmed the conclusions of the writer.

U.S. DEPT. OF AGRICULTURE
WASHINGTON, D.C.

## EXPLANATION OF PLATE VIII

*Bertholletia nobilis* Miers.—The form of the operculum and opercular opening, and the loose, broken cortex are characteristic of this species.

FIG. 1.—Opercula from commercial Brazil nuts; $\times\frac{2}{3}$.

FIG. 2.—Entire pyxidia; $\times\frac{3}{8}$.

FIG. 3.—Pyxidium cut open to show structure; nuts in place; small specimen; natural size.

# BRIEFER ARTICLES

## AN IMBEDDING MEDIUM FOR BRITTLE OR WOODY TISSUES

A mixture of rubber and paraffin as an imbedding medium for brittle objects was first described by J. B. JOHNSTON,[1] and the following is a modification of his original formula.

Melt 98 grams of paraffin of the melting point usually used, to it add 0.4 gram of asphalt (mineral rubber) and heat until the asphalt is dissolved, giving the paraffin a dark color. The purpose of the asphalt is to increase the power of the paraffin to dissolve rubber. For very woody tissue so much asphalt may be added that the paraffin becomes black. To the dark-colored liquid paraffin add 2 grams of crude rubber cut into very small pieces, and keep the mixture at a temperature of 95° C. for several hours, or at the melting point of the paraffin for several days until the solution is saturated with rubber. Then decant the clear supernatant liquid and allow it to cool. Use the dark solid exactly as paraffin is used.

There are two points which require care in manipulation. First, as the rubber tends to separate out slowly if the mixture remains in the melted condition too long, allow the mixture to cool when not infiltrating; second, the elasticity of the mixture leads to the formation of internal air bubbles if the "blocks" containing the imbedded object are cooled too rapidly. During winter, when the water is very cold, it is best not to immerse the blocks completely, but simply let them rest on the surface until hard. The addition of the rubber decreases the melting point of the mixture by two or three degrees.

The relative amounts of the different components of the mixture can be modified to suit individual requirements, and with a little practice the results obtained equal those obtained with the much more cumbersome celloidin method.—H. M. BENEDICT, *University of Cincinnati.*

[1] Journ. Micr. and Lab. Methods **6**: 2662. 1903.

# CURRENT LITERATURE

## BOOK REVIEWS

### Plant and animal breeding for secondary schools

There has been a growing demand in recent years that the secondary schools, especially those located in rural districts, shall give courses in agriculture, domestic economy, and other subjects bearing a practical relation to the life of the people in whose midst the schools are located. In several states these subjects are now a part of the prescribed course. Such requirements make demands for properly trained teachers and for suitable textbooks. A well-conceived and charmingly written manual of plant and animal breeding has been prepared by Professor EUGENE DAVENPORT[1] to partially meet this growing need.

In some respects this work is essentially an abridgment of the same author's earlier work on *Principles of breeding*, but less attention is given to philosophical discussions and more to facts regarding the origin and history of the various domesticated races. Several early chapters describe the manner in which plants and animals came to be domesticated, and point out the need of their further improvement. A chapter on the "ways of the wild" gives a very readable discussion of natural selection and the survival of the fittest, thus giving a basis for a proper appreciation of the relation between artificial selection and the natural evolutionary processes. The principles which are involved in the improvement of plants and animals are then discussed at some length, chief attention being given to GALTON'S *Law of ancestral heredity* and the correlation table.

MENDEL'S laws are given very inadequate treatment. The author evidently has hazy conceptions of unit characters, dominance and recessiveness, latency, atavism, mutation, etc., and his discussions involving these subjects lack the definiteness and accuracy which characterize the rest of the book. He repeatedly emphasizes the statement that each individual possesses all the characteristics of all its ancestors, a statement directly opposed to all Mendelian experience. This lack of precision in the treatment of the principles of Mendelian heredity constitutes the most fundamental defect of the book. It is not only too plainly apparent in the discussions, but is also seen in a number of erroneous definitions in the glossary, as the following examples plainly show: "Gamete, the fertilized ovum"; "Mutant, an individual or

[1] DAVENPORT, E., Domesticated animals and plants. A brief treatise upon the origin and development of domesticated races, with special reference to the methods of improvement. pp. xiv+321. *figs.* 49 and frontispiece. Boston: Ginn & Co. 1910.

strain essentially new and produced spontaneously by nature through crossing, bud variation, or otherwise, synonymous with the older term 'sport'"; "Zygote, that portion of the gamete which determines a unit character." It seems unfortunate that a book otherwise so admirable should propagate such definitions as these. However, the defect in regard to Mendelian heredity is mainly a "sin of omission," and the prepared teacher can easily fill in the vacancy, especially with the aid of PUNNETT'S *Mendelism*. DAVENPORT'S book can not fail to interest, instruct, and inspire, and is deserving of a wide distribution.—GEO. H. SHULL.

**Popular manuals**

The scientific men and women of England have always been interested in interpreting the result of science to the intelligent public not trained in science. Even their scientific papers are apt to be more popular in form than are those prepared in the United States. We cannot but feel that science in America has suffered very much from lack of proper interpretation. Those who are willing to write on scientific subjects for popular reading are usually unfit for the task; and those who are fit, are unwilling. The projected *Cambridge Manuals of Science and Literature* furnish a notable illustration of the continuous effort in England to interest the public in scientific matters. They are not intended primarily "for school use or for young beginners," but also for educated readers who want brief and simple, and at the same time authoritative statements of recent discoveries. The five volumes now issued, dealing with science, will indicate the subjects treated and the kind of authors preparing them.

*The coming of evolution*, the story of a great revolution in science, by JOHN W. JUDD (171 pp.); *Heredity*, in the light of recent research, by L. DONCASTER (140 pp.); *Plant-animals*, a study in symbiosis, by FREDERICK KEEBLE (163 pp.); *The natural history of coal*, by E. A. NEWELL ARBER (163 pp.); *Plant life on land*, considered in some of its biological aspects, by F. C. BOWER (172 pp.).

To issue such a series, at one shilling a volume, is to place this material in the hands of a very wide range of readers, and must react favorably upon the general interest in science.

Another series, having the same purpose, is called *Home University Library*, ten volumes of which have now appeared. It is an English series (Williams and Norgate), as one might expect, published in this country by Henry Holt and Company. The books are larger than the Cambridge Manuals (uniformly 256 pp.), selling for 75 cents, and are more pretentious in contents, suited doubtless to a somewhat better trained group of readers. Four of the volumes are of interest to botanists, as follows: *Modern geography*, by MARION I. NEWBIGIN; *Polar exploration*, by W. S. BRUCE; *The evolution of plants*, by D. H. SCOTT; *Evolution*, by PATRICK GEDDES and J. ARTHUR THOMSON.

A third series is the *Appleton's Scientific Primers*, edited by J. REYNOLDS GREEN, an English botanist. Three of this series have appeared, the third by the editor and entitled *Botany*. It is written from the English point of view, which lays much stress on details and terminology, but is effective in presenting the plant as a living organism, for the author is a physiologist. A great deal of material is packed in the 128 pages, and it would be interesting to know the impression such material makes upon those without laboratory experience.—J. M. C.

## Mendelism

PUNNETT's little book[2] on Mendelism, which was one of the first attempts at a simple popular presentation of its subject, has been completely rewritten and enlarged for its third edition. It is in fact a new book, written however from the same point of view and for the same circle of readers. The author limits himself to the presentation of illustrative examples, with no attempt at exhaustiveness in any phase of the subject, referring readers to BATESON's book on *Mendel's principles of heredity* for more detailed information and for references to the literature. The material used to illustrate the various principles is well chosen, and is mostly derived, as might be expected, from the work of the Cambridge group of geneticists, of which the author is one. This results in a decided advantage, since the author's familiarity with his material favors clarity and vividness of presentation. The slight sense of provincialism given by this method is in this way more than compensated for.

While the treatment is in the main admirable, several unfortunate errors have crept in. It is stated (p. 2) that "among animals the female contributes the ovum and the male the spermatozoon; among plants the corresponding cells are the ovules and pollen grains." Several other zoological writers on genetic subjects have obviously made the same mistake. The animal ovum (after maturation) and spermatozoon are homologous cells, but ovules and pollen grains are not single cells, and not even homologous structures, the ovule consisting mostly of maternal somatic tissue, and the pollen grain being a much reduced gametophyte. The embryo sac within the ovule, and the sperm nuclei in the pollen tube, approximately correspond to the ovum and spermatozoa. On page 51, line 16, *c* should be *C*, and in fig. 8 on the following page the three squares which are black should be albino, and the three marked "albino," but containing *C*, should be black. The author assumes that dominance of a character always indicates that such character is due to something added to the recessive form, thus ignoring the possibility pointed out several years ago by the reviewer[3] that the positive character may be reces-

[2] PUNNETT, R. C., Mendelism. Third edition, entirely rewritten and much enlarged. pp. xiv+192. *pls. 6* and frontispiece. *figs. 32*. New York: The Macmillan Co. 1911.

[3] The "presence and absence" hypothesis. Amer. Nat. **43**:410–419. 1909.

sive through the failure of the unpaired gene in the heterozygotes to produce a visible effect.

A number of excellent text figures and six plates, five of them colored, add greatly to the attractiveness of the book, and the press work leaves nothing to be desired.

This little manual is worthy of an even larger measure of the appreciation which has been given to its two preceding editions by those engaged in other scientific fields, and by general readers who are not themselves engaged in science, but who like to keep themselves informed on the advances that are being made in science.—GEO. H. SHULL.

## MINOR NOTICES

**Alpine plant life.**—In an attractive volume intended for the general reader, ARBER[4] has described the plant life of the higher altitudes of the Swiss Alps. The plants are treated in ecological groups, and an evident effort has been made, not unsuccessfully, to maintain the ecological point of view throughout. It might be questioned if most modern ecologists would find as many beautiful adaptations as are evident to the author, who declares that not only the color of the flowers, but the density of their pigment "may be primarily due to a specialization in favor of a particular class of insect visitor." Other adaptations of alpine plants receive considerable attention, and the probable origin of the alpine flora is briefly discussed.

The text is pleasing in style, the descriptions are accurate and profusely illustrated by more than 75 excellent plates and figures. A glossary of botanical terms and a chapter on the structure of the flower should make all the descriptions intelligible even to the reader who is entirely without scientific training.—GEO. D. FULLER.

## NOTES FOR STUDENTS

**Cecidology.**—The anatomy and histology of insect galls continues to be an interesting and profitable field not only for the entomologist, but also for the plant pathologist and the experimental biologist. WEIDEL[5] gives us a valuable study of the life history of the gall of *Neuroterus vesicator* Schlecht. He first calls attention to the failure thus far to explain experimentally the reason for gall formation, and the necessity of comparing the structure of the gall with the normal structure of the plant. After briefly reviewing the history of the study of the gall structures, especially the studies of BEYERICK, who attributed the gall characters which are recognized by the zoologist to a "growth enzyme," he discusses his methods. These methods are well worthy

[4] ARBER, E. A. NEWELL, Plant life in alpine Switzerland. 8vo. pp. xxiv+355. *pls. 47. figs. 30.* London: John Murray. 1910. $1.50.

[5] WEIDEL, F., Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie der Cynipidengallen der Eiche. Flora **102**: 279–334. *pl. 15. figs. 49.* 1911.

of notice by our American workers. The mature galls were taken into the laboratory and the insects hatched. These insects were then imprisoned in glass cylinders with leaves and buds of the oak, and the oviposition observed. The material was then fixed in Flemming's fixer at various intervals following oviposition, and sectioned. He confirms the observations of BEYERICK on the ovipositions, and states that in this species the female does not puncture the plant tissue. The "growth enzyme" is from the larva, and the gall formation begins with the hatching of the larva, which becomes inclosed by a cell growth within about 24 hours. In the second part of this paper the author makes a comparative study of the sclerenchyma cells of a number of galls. He also states that the character depends somewhat upon the part of the host plant on which the gall is formed.

KÜSTER[6] gives a brief discussion and criticism of one of TROTTER'S[7] recent papers, in which he compares the protoplasmic and histological characters of certain galls with the primary axis of the dicotyledonous plants. He agrees in part, and cites the great similarity between galls and fruits as evidence. He calls attention to the necessity of comparative study of the structure of gall with the normal structure of the plant. The galls and dicot stems both have the radial arrangement of parts, with parenchyma tissue in the center, but the fibrovascular bundles of the galls are not so well developed as in the stems. KÜSTER sees enough differences in structural characters to prevent agreement with TROTTER, but does not go into an extended discussion of these differences.

GREVILLIUS[8] gives a very interesting discussion of certain pseudo-galls or Thysanopterocecidia. The first of these was briefly described by RUBSAAMEN in 1901. The author agrees with RUBSAAMEN, but gives a more detailed discussion. The insect attacks the upper surface of the leaf, causing the tips to curl. The upper epidermis is seriously injured and the mesophyll somewhat distorted, but the palisade cells only slightly changed. The mesophyll is poorer in chlorophyll than in the normal leaves. When the buds are attacked they fail to develop. A similar gall not previously described occurs on *S. graminea*. A Thysanopterocecidia on the *Polygonum Convolvulus* is also described, but in this the insect attacks the under surface of the leaves. The structural characters are practically the same as the preceeding.

The LEEUWEN-REIJNVAANS[9] give a fourth paper on the cecidia of Java,

[6] KÜSTER, ERNEST, Ueber die Sprossähnlichkeit der protoplasmatischen Gallen. Marcellia **9**:159, 160. 1911.

[7] TROTTER, A., Sulla possibilita di una omolgia caulinare nelle galle prosplastiche. Marcellia **9**:109. 1911.

[8] GREVILLIUS, DR. A. Y. VON, Notizen ueber Thysonopterocecidien auf *Stellaria media* Cyr., *S. graminea* L., und *Polygonum Convolvulus* L. Marcellia **9**:161–167. 1910.

[9] LEEUWEN-REIJNVAAN, J. und W. DOCTORS, Einige Gallen aus Java. Vierter Beitrag. Marcellia **9**:168–193. 1911.

in which they describe 50 specimens, most of which are caused by insects of the genus *Cecidomyia*. This material was collected in the Oengaran mountains at an elevation of 700 to 1000 meters. Large, soft galls with water parenchyma were especially abundant.

TROTTER[10] gives brief descriptions of 24 species of galls collected by Dr. FORTI in Asia Minor, and occurring on *Quercus aegilops* L. (*Q. vallonea Kosch.*), *Q. lusitanica* Lan., and *Rosa* sp. Most of these species had already been described.

KIEFFER (Bitsch) and HERBST (Valparaiso)[11] describe seven new species of cecidia and insects producing them, from Chile, and give brief descriptions of those species not previously described.

Among the papers on American cecidology we note FELT'S[12] key, parts of which will be serviceable to the botanist as well as to the entomologist, but there are not enough characters of the galls given to enable exact determinations.

EDITH M. PATCH[13] gives a most excellent piece of work on the aphis galls of the elms. Although, with the exception of brief descriptions of the galls, the major part of the work is devoted to the biology and life history of the insects, the work is of great value to the botanist. Several species which have previously been very much confused are separated in a manner which makes them easily distinguishable. The value of the work is increased by the illustrations and bibliographies.

SMITH'S[14] bulletin comes to us as a valuable contribution on bacteriocecidia. The historical discussion and the long series of experiments are interesting and valuable. It is very doubtful if any cecidia have a wider range of host plants than has been proven for this one. The fact that the galls are produced most readily in soft, rapidly growing tissues, is in harmony with results already obtained by the study of insect cecidia, and further studies will doubtless bring out other similarities. The very limited discussion given to the stimulus and to the character of the cecidia leads us to hope for another bulletin in which these phases of the subject will receive more attention.

NORTON[15] records a very interesting crown swelling of the peach due to

[10] TROTTER, A., Pugillo di Galle Roccolte dal Dr. A. FORTI in Asia Minor. Marcellia **9**:193–197. 1911.

[11] KIEFFER, VON, und HERBST, P., Ueber Gallen und Gallenthiere aus Chile. Cent. f. Bakt. Paras. u. Infek. **29**:696–704. 1911.

[12] FELT, E. P., Gall midges of *Aster*, *Carya*, *Quercus*, and *Salix*. Jour. Econom. Ent. **3**:347–356. 1911.

[13] PATCH, EDITH M., Gall aphids of the elm. Bull. No. 181, Maine Agric. Experiment Station. 1911.

[14] SMITH, E. F., BROWN, N. A., and TOWNSEND, C. O., Crown gall of plants; its cause and remedy. Bur. Plant Industry, Bulletin 213. 1911.

[15] NORTON, J. B. S., Crown swelling disease of peach. Phytopathology **1**:53, 54. 1911.

unknown causes. The structure of the swelling is characterized by spongy masses of parenchyma filled with starch and interspersed with woody layers.

An interesting myco-cecidia of the orange is described by FLORENCE HEDGES.[16] This cecidia is attributed to *Sphaeropsis tumefaciens*, nov. sp., which is described. The external characters of the gall are given, but the development and histology are omitted.—MEL T. COOK.

**Phycomycetes.**—PETERSEN gives an abbreviated English translation of his paper on the aquatic Phycomycetes of Denmark, which was originally published in Danish. The paper[17] is divided into three parts, the first dealing with the phylogeny and relationships of the Phycomycetes, the second with their occurrence and distribution, and the third with descriptive taxonomy.

As to their phylogeny, the author adheres to the view that the aquatic Phycomycetes and their near relatives constitute a phylogenetic series. If they were derived from the algae at various levels, they would hardly show the homogeneity which runs through the aquatic forms. As to the direction of their evolution, he holds that the lower Phycomycetes have been derived from the higher forms through reduction of the plant body. This view, which necessitates the assumption that motile zoospores and cilia were acquired by the degenerating forms, meets with difficulty when the non-aquatic Peronosporales are considered. The author regards the Pythiaceae, on account of their probable relationship with *Lagenidium*, as the ancestors of Lagenidiaceae. The Peronosporales, to which the Pythiaceae belong, would therefore form a part of the reduction chain, and it would be necessary to assume that zoospores adapted to aquatic conditions have arisen among the aerial Peronosporaceae from conidia eminently suited for aerial distribution. The alternate hypothesis that the Peronosporaceae are losing their aquatic characters in a dry habitat, instead of acquiring them, seems more reasonable. The chief argument of the author is directed against the view of FISCHER that the Phycomycetes are derived from the Monadineae. Here he rightly points out, among other differences, that the germinating zoospore of the Phycomycetes leaves the spore membrane behind, while in the endophytic Monadineae the zoospore makes its way in its entirety into the host cell. The author rightly regards the Synchytriaceae as a distinct group, which represents a line of development different from the rest of the Chytridiales. The idea is not fully carried out, however, in his synopsis of the families given later.

In the second part of the paper are given many interesting observations on the biology and distribution of the aquatic Phycomycetes in Denmark. The Saprolegniales occur frequently on fish and frog spawn, but they do not

[16] HEDGES, FLORENCE, *Sphaeropsis tumefaciens*, nov. sp., the cause of the lime and orange knot. Phytopathology **1**:63–65. 1911.

[17] PETERSEN, H. E., An account of Danish freshwater Phycomycetes, with biological and systematical remarks. Ann. Myc. **8**:494–560. *figs. 27*. 1910.

———, Studier over Ferskvands-Phycomyceten. Botanisk Tidsskrift **29**: 345–429. *figs. 27*. 1909 (with English abstract).

produce such epidemics among fish as have been reported in other countries. Dead twigs, which have fallen into the water near the shore, form the most common habitat for these fungi. They sometimes occur on remains of aquatic plants, like *Nuphar* and *Nymphaea*, but herbaceous plants do not generally seem to be a favorable substratum for their growth. Leaves which fall into the water in autumn are not a suitable subtratum. The lower forms frequently infect plankton crustaceans, which have not generally been regarded as hosts for these fungi. The most favorable time for the growth of the aquatic Phycomycetes is in early spring, while the water is still too cold to allow growth of bacteria and infusoria.

The rest of the paper consists of a taxonomic arrangement of the species, with notes as to their habits and occurrence. The brief descriptions which are given for the known species in the former paper are omitted in the translation, diagnoses being given only for the new species. Of these there are twelve. One, *Pythiomorpha gonapodyoides*, represents a new generic type. It is unfortunate that the designation "sp. nov." accompanies the names of these species in the translation. It is needless to point out the confusion that may result from such double publication of new species in editions appearing nearly a year apart.

The paper, which is an excellent achievement in local botany, shows the results which sustained study of a group may be expected to yield in territory of which the flora is presumably fairly well known. It is to be hoped that it may direct the work of botanists of other countries to this fruitful field.

According to a brief article by MAIRE and TISON,[18] sexuality usually attributed to *Urophlyctis* is lacking in that genus. In *Urophlyctis* empty cells are found accompanying the sporocysts, thus making it appear as if conjugation had taken place. These empty cells, however, according to the authors, are nothing more than the older vegetative cells whose contents have passed into the younger cells, which arise as buds from the older ones. The authors conclude that *Urophlyctis* should be classed with the Cladochytriaceae, the three genera, *Urophlyctis*, *Physoderma*, and *Cladochytrium*, forming a well-defined natural group.

LECHMERE[19] has described the abnormalities occurring in a species of *Saprolegnia* which he had under observation in pure cultures for a period of five months. The abnormalities, which frequently occur in laboratory cultures of these plants and some of which have been figured by several investigators, occur mostly in the sporangia, and cause these organs to assume forms and modes of behavior characteristic of other genera of the Saprolegniales. Variations are described simulating the sporangia of *Leptomitus*, *Pythiopsis*, *Achlya*,

[18] MAIRE, RENÉ, et TISON, ADRIEN, Recherches sur quelques Cladochytriaceae. Compt. Rend. **152**:106, 107. 1911.

[19] LECHMERE, A. F., An investigation of a species of *Saprolegnia*. New Phytologist **9**:305–319. *pls. 1, 2.* 1910.

*Dichtyuchus*, and *Aplanes* in form, manner of discharge, and germination of spores. A common type of variation is one in which chains of rounded sporangia discharging laterally are formed. It is well to have these variations recorded from observations on a single form in pure cultures.—H. HASSELBRING.

**Photosynthesis in water plants.**—BLACKMAN and SMITH[20] have published two papers upon "Gaseous exchanges of submerged plants," being nos. 8 and 9 of the excellent series on "Experimental researches on vegetable assimilation and respiration" issued from BLACKMAN's laboratory. The first of the present papers deals with "A new method for estimating the gaseous exchange in submerged plants." Instead of using the oxygen elimination as the basis for study, the $CO_2$ consumed is determined. Water of known $CO_2$ content (determined by tritation) is passed over submerged plants of a given illuminated surface, and the $CO_2$ withdrawn for photosynthesis determined by later titration. Correction is made for $CO_2$ produced by respiration and for that in the eliminated gas. The method seems to insure reasonable accuracy.

In agreement with other workers, BLACKMAN and SMITH find *Elodea* extremely sensitive to adverse conditions. A few days of storage in tap water in laboratory or greenhouse cuts the assimilation 17 to 30 per cent. The plant also endures great concentration of $CO_2$. Water saturated from an atmosphere containing 30 per cent $CO_2$ does not interfere with assimilation; it is not likely that air plants would long endure such concentrations. The points of large significance can be set forth by quotations from the summary of the second paper:

"The aim of this study is to demonstrate the *nature* of the relation between assimilation and the chief environmental factors: (1) $CO_2$-supply, (2) light-intensity, and (3) temperature. The relation is such that the magnitude of this function in every combination of these factors is determined by one or the other acting as a limiting factor."

"The identification of the particular limiting factor in any definite case is carried out by applying experimentally the following general principle. When the magnitude of a function is limited by one of a set of possible factors, increase of that factor, and of that one alone, will be found to bring about an increase of the magnitude of the function."

"The experiments in this paper deal with such moderate intensities of assimilation as may be fairly well maintained for several successive hours. With more intense assimilation the values soon fall off by the action of internal factors grouped at present as the *time factor*. Experiments in which this additional factor has to be reckoned with will be considered in a later paper."

[20] BLACKMAN, F. F., and SMITH, A. M., Experimental researches on vegetable assimilation and respiration: VIII. A new method for estimating the gaseous exchanges of submerged plants; IX. On assimilation in submerged water plants and its relation to the concentration of carbon dioxide and other factors. Proc. Roy. Soc. London B **83**:374–412. 1911.

The work from BLACKMAN's laboratory has done much to substitute a physico-chemical conception for the too general stimulus conception of the German plant physiologists. In this direction these papers again bring forth evidence for the non-existence of true optima, for the great importance of "limiting factors," and for the significance of what BLACKMAN has designated as the "time factor."—WILLIAM CROCKER.

**Cytology of the ascus.**—The controversy to which the behavior of the ascus nucleus has recently given rise, has led GUILLIERMOND[21] to reinvestigate the subject. Contrary to the results of Miss FRASER[22, 23, 24] and her coworkers, these new observations extend and entirely confirm his previous studies, and convince him that the number of chromosomes remains constant during the three successive mitoses of the ascus nucleus. He discusses the method of formation and the separation of the chromosomes of the first division, and whether there exists a second numerical reduction during the third nuclear division. In all of the species studied (*Humaria rutilans*, *Peziza catinus*, *Pustularia vesiculosa*, *Galactinia succosa*), he finds that the number of chromosomes of the equatorial plate stage and of the anaphases remains the same, and that the distribution of these chromosomes is accomplished in the same way in all of these forms. As in previous studies, GUILLIERMOND[25, 26] believes that the process described by MAIRE[27, 28] that is, a double longitudinal division of the chromosomes during the anaphases, which results in doubling the number of chromosomes found in the equatorial plate stage, rests on incorrect observations. He also believes that MAIRE's contention that there exists in the ascus of *Galactinia succosa* protochromosomes, which fuse into four definite chromosomes, is untenable. GUILLIERMOND holds that there are eight definite chromosomes and not four, which are formed directly and not from protochromosomes. These eight chromosomes are divided only during the meta-

[21] GUILLIERMOND, M. A., Aperçu sur l'évolution nucléaire des ascomycètes et nouvelles observations sur les mitoses des asques. Rev. Gén. Botanique **23**:89–120. 1910.

[22] FRASER, H. C. I., Contributions to the cytology of *Humaria rutilans*. Ann. Botany **22**:35–55. 1908.

[23] FRASER, H. C. I., and WELSFORD, E. J., Further contributions to the cytology of the ascomycetes. Ann. Botany **22**:465–477. 1908.

[24] FRASER, H. C. I., and BROOKS, W. E. ST. J., Further studies on the cytology of the ascus. Ann. Botany **23**:538–549. 1909.

[25] GUILLIERMOND, M. A., Recherches sur la karyokinèse des ascomycètes. Rev. Gén. Botanique **16**:1–65. 1904.

[26] ———, Remarques sur la karykinèse des ascomycètes. Ann. Mycol. **3**:344–361. 1905.

[27] MAIRE, R., Recherches cytologiques sur quelques ascomycètes. Ann. Mycol. **3**:123–154. 1905.

[28] ———, Recherches sur la karyokinèse chez les ascomycètes. Rev. Gén. Botanique **16**:130–143. 1904.

phases, and not again during the anaphases. The exact manner of division of the chromosomes seems to agree with that described by Miss FRASER, but on the basis of certain stages, which he thinks were missed by her, he interprets his results in a different way. He describes a synapsis stage, whose loops correspond to the V-shaped chromosomes, which later appear on the spindle in the equatorial plate. Although he does not very strongly insist on this point, he is inclined to think that the scheme of chromosome reduction described by FARMER and MOORE for higher forms of plants and animals obtains in the ascomycetes. In the first part of the paper an interesting discussion of the state of these questions and other problems relating to the ascomycetes will be found.—J. B. OVERTON.

**Anaerobic growth.**—LEHMAN[29] has studied anaerobic growth in higher plants, trying to determine whether the view of WIELER or that of NABOKICH is correct. WIELER claims that the higher plants will not grow in total absence of oxygen, but that only a very low oxygen pressure is needed for growth. NABOKICH claims that higher plants will grow in absence of oxygen. He maintains, however, that proper nutritive conditions must be supplied, as in fungi. For this purpose a glucose solution is suitable. This solution certainly increases anaerobic growth in the pea seed, sunflower seedling, and other forms. In a later article, not cited by LEHMAN, NABOKICH[30] describes the course of anaerobic growth in higher plants. Soon after placing the organ in the oxygen-free medium, growth ceases (Vacuumstarre). Somewhat later growth begins, and the rate rises until it equals that of aerobic growth. Still later growth ceases and death of the organ ensues. NABOKICH explains the course of anaerobic growth as follows: oxygen acts as a stimulus to growth, and not merely as an energy releaser, hence with its withdrawal growth ceases; intramolecular respiration later produces poisonous by-products, which in low concentrations act as stimuli to growth, but which with further accumulations stop growth and kill the organ. The bad feature of this explanation is the indefiniteness of the term stimulus. NABOKICH finds that resting plant cells or those with low metabolic activity can remain in oxygen-free condition for long periods without injury.

LEHMAN found only very slight if any anaerobic growth in *Vicia Faba*, *Pisum sativum*, *Lupinus albus*, *Brassica Napus*, *Phaseolus multiflorus*, and *Cucurbita*, either in distilled water or glucose solution. In *Zea Mays* and *Glyceria fluitans*, anaerobic growth was marked in glucose solution, but was nil in distilled water. In *Helianthus annuus*, anaerobic growth was slight in distilled water, but considerable in glucose solution. LEHMAN concludes that anaerobic growth in any higher plants is not long-enduring nor considerable

[29] LEHMAN, ERNST, Zur Kenntnis des anaeroben Wachstums höheren Pflanzen. Jahrb. Wiss. Bot. **49**:61–90. 1911.

[30] NABOKICH, A. J., Ueber die Wachstumsreize. Beih. Bot. Centralbl. **26**:7–149. 1910.

when compared with aerobic growth. He also finds no coincidence between intensity of "intramolecular" respiration and of anaerobic growth. The conclusions of these workers are drawn from too few and these mainly cultivated forms. Study of wild forms of varied habits may show very different results. —WILLIAM CROCKER.

**Structure of the spore wall.**—A notable addition to our knowledge of the structure and development of the spore wall is contributed by BEER[31] in a study of the young pollen grains of *Ipomea purpurea*. At the conclusion of the reduction division, the tetrads of young pollen grains become surrounded by massive mucilaginous walls, which show the reactions of callose and pectose. Within this mucilaginous wall, and surrounding each young pollen grain, is another mucilaginous wall with the same reactions. This second wall is called the "special wall," a term suggested by STRASBURGER to replace the awkward and misleading term "special mother cell wall." The exine is deposited by the pollen protoplast upon the inner surface of the special wall, and at first is homogenous, but soon becomes differentiated into an outer lamella, with a network of thickening bands on its inner surface, and at the intersection of the bands are the rudiments of the spines. At this stage a clear space is seen between the outer lamella and the thickening bands, and in this space the rodlets characteristic of the mature pollen develop. The spines project into the pollen cavity before they begin to appear externally. The intine develops within the exine as a thin layer, with thicker portions where it protrudes into the exit pores. Chemically, it consists of pectic bodies associated with some cellulose. In older pollen grains the exine consists of a delicate outer lamella perforated with countless pores, so that it really forms a reticulum with open meshes, beneath which are the thickening bands constituting the mesospore, perforated by the narrow exit pores for the pollen tubes. The outer lamella of the exine dips into the exit pores and covers the protrusions of the intine at these spots. Since nearly the entire growth of the rodlets and spines takes place after they have become separated from the protoplast, it is concluded that they are able to develop without any direct contact with the protoplasm.

This short paper presents a thorough study of a single species and suggests a series of investigations, for it may be predicted with the utmost confidence that the account will not hold for angiosperms in general, and the author makes no such claim. After various types of pollen grains have received similar attention, it will be time to generalize.—CHARLES J. CHAMBERLAIN.

**Chemotaxy.**—SHIBATA[32] gives the first part of a full statement of his extensive work on chemotactic responses of the spermatozoids of pteridophytes. This

[31] BEER, RUDOLF, Studies in spore development. Ann. Botany **25**:199–214. *pl. 13*. 1911.

[32] SHIBATA, K., Untersuchungen über die Chemotaxis der Pteridophyten Spermatozoiden. Jahrb. Wiss. Bot. **49**:1–60. 1911.

part deals with positive reactions, while the second part will deal with the negative. SHIBATA himself has contributed no small part of the knowledge in this field, especially with the forms *Isoetes*, *Salvinia*, and *Equisetum*. The paper is divided into seven sections dealing with the following phases of the subject: (1) introduction and methods, (2) action of organic acids, (3) action of metallic ions, (4) action of H and OH ions, (5) action of alkaloids and other organic bases, (6) application of the Weber-Fechner Law, (7) the classes of chemotactic sensibility and their relation to each other.

The body of facts is so great that no statement of it can be attempted here. Some of the generalizations, however, especially those derived from the seventh section, are of considerable interest. SHIBATA concludes that there exists in the pteridophytes three categories of positive chemotactic sensibility: (1) for the anions of malic acid and of the related dicarboxyl acids, (2) for the OH ion (only in *Isoetes*), (3) for cations of metals and hydrogen and for alkaloids. The three categories are entirely independent, as indicated by the lack of antagonistic action between members of different categories. Within the same category one member dulls the action of any other. In general, the dulling effect is proportional to the attractive value, but this is not always the case. Citrate, which is 1/10 as powerful in attracting *Salvinia* sperms as is maleate, is just as effective in dulling the action of maleate as is maleate itself. SHIBATA believes that in chemo-perception within a given category either the first links or at least early links in the chain of perception are identical. He contrasts this situation with that found by KNIEP in certain bacterial forms, who concluded that each individual substance is separately perceived. He found no dulling action between any two chemotactically active substances.—WILLIAM CROCKER.

**Coremia formation by Penicillium.**—By methods which at the present stage of plant physiology appear somewhat crude and superficial, WÄCHTER[33] has attempted to find the factors influencing the formation of coremia in a form of *Penicillium*, which he designates by the usual name of *P. glaucum*, but which can be easily identified as *P. expansum* Link. The method of study consisted in growing the fungus on sterilized slices of various fruits and vegetables, and on the expressed juices of these, and also on an inorganic nutrient solution with various concentrations of sugar, this being the only medium approximating anything like known conditions. When the results are sifted, we are left in the same position as before as to the factors which influence the formation of coremia, namely, that when grown on various substrata of unknown composition this form (like other coremia-forming species) sometimes forms coremia and sometimes not, a fact, moreover, clearly formulated by THOM[34] in regard to this and other species of similar habit. The work of

[33] WÄCHTER, W., Ueber die Koremien von *Penicillium glaucum*. Jahrb. Wiss. Bot. **48**:521–548. 1910.

[34] THOM, CH., Cultural studies of species of *Penicillium*. U.S. Dept. Agr., Bur. Animal Industry, Bull. 118. 1910.

THOM, however, came to the author's hands only in time to be noted in the proof. A closer approximation to definitely known conditions, if not yielding positive results, might at least have resulted in excluding certain groups of factors as having no influence on the formation of coremia.

In the latter part of the paper, the author distinguishes 11 forms of *Penicillium* by their growth characters on the substrata which he used in the first part. The forms are not further characterized nor identified with other descriptions. The author lays stress on cultural characteristics, and the utilization of the coremia-forming habit for separating the species of *Penicillium*. Both have been used by THOM in his partial monograph of the group. —H. HASSELBRING.

**Feed containing smut spores.**—The feeding of grain products containing large quantities of smut spores to animals has usually been regarded as pernicious, both on account of the widespread belief, supposed to be based on practical experience, that the smut spores are injurious to animals, and on account of the danger that the spores pass uninjured through the animal body and, as asserted by BREFELD, become a source of infection when they are distributed over the fields in manure. These questions have been reinvestigated by HONCAMP and ZIMMERMANN,[35] who as a result of feeding experiments, in which large quantities of smut spores, mostly of *Tilletia caries* with some of *T. laevis*, were fed to different domestic animals for long periods of time, came to the conclusion that in no case could any injury be definitely attributed to the smut spores. The spores which had passed through the bodies of animals, with rare exception, were incapable of germination. Further experiments showed that sound spores mixed with manure or other fertilizers and scattered over the soil rarely cause infection of grain. These experiments indicate that the danger of infection from smut spores scattered over the fields in manure has been largely overestimated. This is true more particularly of the spores that have passed through the animal body. The only source of infection to be regarded of significance in agricultural practice is that from the spores adhering to the seed grain, a fact which may be inferred from the almost total prevention of smut by treatment of the seed grain.—H. HASSELBRING.

**Temperate plants in Helgoland.**—Since the spring of 1904, KUCKUCK has been experimenting with the introduction into Helgoland of various species of plants of warm temperate climates.[36] Although situated but 30

[35] HONCAMP, FR., und ZIMMERMANN, H. (unter Mitwirkung von G. SCHNEIDER), Untersuchungen über das Verhalten von Brandsporen im Tierkörper und im Stalldünger. Centralbl. Bakt. II. **28**:590–607. 1910.

[36] KUCKUCK, P., Ueber die Eingewohnung von Pflanzen wärmerer Zonen auf Helgoland. Bot. Zeit. **68**[1]:49–86. *pls. 1–3. figs. 2.* 1910.

km. from the mainland, this island enjoys many of the features of an insular climate. February, the coldest month, has a mean temperature of only 1°.34 C., and the lowest temperatures of the winter seldom exceed −8° C. This is much milder than the climate of the mainland, but less genial than that of the southern coast of England. Notwithstanding the favorable temperatures, many plants are injured by the severe and incessant winter winds, and by the lack of a protective covering of snow. KUCKUCK describes his results in detail, indicating the successful culture in the open of a large number of species, including such plants as *Pittosporum Tobira*, *Camellia japonica*, two species of *Fuchsia*, and various opuntias. Perhaps the most noteworthy of them is the fig, *Ficus carica*, which has been cultivated on the island for thirty years, attains a height of 4.5 meters, and matures fruit regularly. KUCKUCK considers in general that the winds are more hostile to plant life than the frosts, and believes that other species might prove hardy if they could be given soils better suited to their requirements.—H. A. GLEASON.

**Twining.**—NIENBURG[37] has made a detailed study of the nutation movements of young twining plants in their early stages of circumnutation. He believes that all the circumnutation and twining movements can be explained by the joint action of autonomic nutation and negative geotropism. He also believes that he has entirely disposed of NOLL's conception of lateral geotropism. A careful analysis of his results, however, shows that lateral geotropism will also explain all movements he describes, with the possible exception of one on the centrifuge. The strongest evidence for NOLL's conception was gained from the use of the centrifuge, and now with a slight alteration of the position of the plant NIENBURG obtains results on this instrument that seem to disprove NOLL's conception. NIENBURG's centrifuge experiments have their main value, however, in showing the need of further centrifuge studies in this field.—WILLIAM CROCKER.

**Amphibious polygonums.**—A recent paper very plainly shows that extensive experimental cultures will be necessary before the taxonomic and ecological relationships of the various species of *Polygonum* can be settled. NIEUWLAND[38] distinguishes at least three closely related species of this interesting genus which exhibit both an aquatic and a terrestrial form, but adds no experimental data to our present scanty fund. The species described vary so much in response to varying conditions of habitat that it seems possible that all these forms, with intermediate gradations, might be produced from the same stock by careful methods of culture. An interesting historical résumé of the litera-

[37] NIENBURG, WILHELM, Die Nutationsbewegungen junger Windepflanzen. Flora 102:117–146. 1911.

[38] NIEUWLAND, J. A., Our amphibious Persicarias. Amer. Midland Naturalist 2:1–24. 1911.

ture shows that our knowledge of the ecology of these plants has advanced but little beyond the observations recorded by JOHN RAY[39] more than two centuries ago.—GEO. D. FULLER.

**Syndiploid nuclei.**—Nuclear figures in chloralized root tips, described by NĚMEC, then by STRASBURGER, and then discussed and figured at some length in NĚMEC's recent book on fertilization, have been reinvestigated by STRASBURGER.[40] He used again the root tips of *Pisum sativum*, and made a critical comparison of the nuclear figures in normal and chloralized tips, and compared the peculiar mitoses of syndiploid nuclei with the normal heterotypic mitoses of the same species. He agrees with NĚMEC that the syndiploid nuclei gradually disappear, but denies that any heterotypic mitoses are concerned in the disappearance. NĚMEC's figures, intended to support the theory of a somatic heterotypic mitosis, are discussed and explained as only peculiar vegetative mitoses, with merely superficial resemblances to genuine reduction divisions. —CHARLES J. CHAMBERLAIN.

**Structure of protoplasm.**—During the last decade cytologists have been so busy with various phases of the chromosome problem that little attention has been given to the structure of protoplasm. A preliminary announcement by LEPESCHKIN[41] is entitled "On the structure of protoplasm," but this paper deals with artificial emulsions rather than with protoplasm itself. The principal conclusion is that streaming protoplasm cannot have the foam structure described by BÜTSCHLI, but rather has the structure of an emulsion. He admits that the peripheral layers of protoplasm in infusoria may have a foam structure.—CHARLES J. CHAMBERLAIN.

**Peat bogs in Iowa.**—A comparison has been made by PAMMEL[42] between the peat bogs of northern Iowa and those occurring in other parts of the United States. The principal types found in this state are the aspen bog, willow bog, sedge bog, and rush bog, none having a very extensive development. The sphagnum bog is conspicuously absent. A detailed comparison of the bog flora of Iowa, Wisconsin, and Michigan shows that in Iowa many of the typical bog plants of more northern regions are replaced by others of a very different character.—GEO. D. FULLER.

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[39] RAY, JOHN, History of plants. Vol. I, p. 185. 1686.

[40] STRASBURGER, EDUARD, Kernteilungsbilder bei der Erbse. Flora **102**:1–23. *pl. 1.* 1911.

[41] LEPESCHKIN, W. W., Ueber die Struktur des Protoplasmas. Ber. Deutsch. Bot. Gesells. **29**:181–190. 1911.

[42] PAMMEL, L. H., Flora of northern Iowa peat bogs. Iowa Geol. Survey **19**: 739–784. 1909.

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